HULL BULLETINS OF MARINE ECOLOGY

VOLUME II

EDITED BY

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LIST OF PERSONNEL OF THE DEPARTMENT OF OCEANOGRAPHY, UNIVERSITY COLLEGE OF HULL, 1941 – 1950

Honorary Director:

Professor A. C. HARDY, M.A., D.Sc.(Oxon.), F.R.S.

Head of Department:

C. E. Lucas, D.Sc.(London), 1931–1948.

(In 1948 Dr. Lucas was appointed Director of Fisheries Research, Scottish Home Department, and Mr. K. M. Rae became the acting Head of the Department.)

Research Biologists:

K. M. RAE, O.B.E., B.Sc.(London), 1935–
(Acting Head of the Department, 1948–1950.)
G. T. D. HENDERSON, D.S.C., B.Sc., Ph.D.(Bristol), 1931–
N. B. Marshall, M.A.(Cantab.), 1937–1947.
C. B. REES, D.Sc.(Wales), 1937–
H. G. Stubbings, M.A., Ph.D.(Cantab.), B.Sc.(London), 1939–1946.
R. S. GLOVER, B.Sc.(Manchester), 1945–
A. Saville, B.Sc.(Aberdeen), 1946–1948.
F. R. VANE, M.Sc.(Liverpool), 1947–
H. R. Schurr, B.Sc.(Glasgow), 1949–1951.

Experimental Officers:

W. W. BROWN, B.Sc.(Leeds), 1948–
G. A. COOPER, 1947–
Miss M. F. JOBSON, B.Sc.(St. Andrews), 1947–
Miss D. E. JOHN, 1947–
Miss D. E. Williams (Mrs. A. Saville), B.Sc.(Wales), 1947–1948.

Laboratory Stewards:

J. SCRIVENER, 1935–
F. H. Dewing, 1937–1949.

Names in italics indicate those members who have left the Department.

EXPLANATION

A non-technical account of the contents of Volume II by the Editors

THE inclusion of this brief introduction to the volume may itself require some explanation and this can most readily be given by quoting from the preface to Volume I :

> " Oceanographic researches must often appear to members of the (fishing) industry to be remotely removed from their immediate interests. Since reports such as the present ' Bulletins,' which are intended primarily as contributions to the scientific literature of the subject, will necessarily be too detailed and technical to be read by the layman, each volume will be accompanied by an explanation of its contents : a non-technical account pointing out its bearing on the future welfare of the industry."

This preface was followed by an explanation which, since it dealt with the very beginnings of the work, was also largely a discussion of the scope and nature of marine ecology in general. It dealt particularly with the importance of the plankton in the understanding of the natural economy of the sea before passing to a description of the methods for its survey which have been developed as a special feature of the present research. This second volume is concerned with a continuation of the work described in the first so that the former explanation will largely serve also for this and need not be repeated ; the general reader who has not yet read that first explanation should refer back to it before going further with the present volume. Since in quoting from the original preface we have referred to the relation of the work to the fishing industry it may be well to repeat also a word or two of caution from the first explanation :

> " We are just at the beginning ; we have a very long way to go before the goals we are working towards can be realized. They must be approached slowly, making sure of the ground step by step ; there will be many temptations to jump to conclusions on too slender evidence. The limitations of the methods we are employing must be carefully weighed and a good deal of space in the coming ' Bulletins ' will be concerned with these. Direct economic results must not be expected quickly. The more immediate outcome will be a better understanding of the nature of the changes taking place in the North Sea plankton community as a whole ; any steps, however, towards a better knowledge of the biology of the North Sea is a step towards ultimate economic advantage."

The first volume described the results of the plankton recorder survey of the North Sea in its early experimental stages from 1932 to 1937 when it was confined to the southern North Sea. The essential feature of the method is the use of a number of machines, the continuous plankton recorders, which, when towed by steamships across the sea, automatically and continuously sample the plankton at a standard depth of 10 metres so that subsequently estimates of the varying quantity of different organisms may be made for the different parts of the sea. By using such instruments at monthly intervals on a number of different lines across the sea knowledge may be gained of the main changes in the distribution and abundance of the principal constituents of the plankton with the passage of time. We want to know how far, in this or that month, conditions in this or that part of the sea are exceptional or not ; only by knowing this can we begin to correlate such deviations from the normal with variations in the fisheries on the one hand and with changing hydrological or weather conditions on the other. Before this can be done, however, many years of observations must be taken and compared in order to establish what may be regarded as the normal state of affairs, or at least, a " standard " from which the deviation can be measured. We are still in this pioneer stage.

The results of the first five years' trial in the restricted region of the southern North Sea were so promising that in 1938 a new laboratory was opened in Leith and the recorder survey was extended by the addition of new lines to cover the greater part of the North Sea ; a year later, in 1939, the first line into the North Atlantic towards Iceland was begun. Then the outbreak of the second world war for the time being brought the whole programme to a stop. The ' Bulletins ' in the present volume, except the last, deal entirely with the results of this expanded survey of 1938 and 1939. ; they show us for the first time, month by month, the main changes in the plankton over practically the whole of the North Sea for a year and eight months. They form an important basis for comparison with the results of the post-war survey, happily revived on an even more extensive scale and to be described in later volumes.

We will now deal briefly with each ' Bulletin ' in turn.

' BULLETIN ' NO. 7.

This requires little explanation, for it is itself a general introduction to this 1938–39 survey. It describes the expansion of the area covered, charts the position of the new lines together with the old, and shows their relation to the varying depth of the sea bed. There is a complete summary list of records as well as a series of charts showing the lines along which successful recording was achieved in each of the twenty months of the survey. In these charts the parts of each record taken between sunset and sunrise are shown by a much thicker line than those parts taken in the day-time ; this enables one to compare them with the plankton distribution charts which follow in later ' Bulletins ' to see whether some of the results may be effected by the diurnal changes in the vertical distribution of some of the animals. This is one of the possible limitations to the method to which a good deal of attention has been given in these 'Bulletins'; actually it is found that this effect is of significance in only a comparatively small number of species and its importance is discussed in the subsequent 'Bulletins' concerned. During this twenty-month period 188 records were made covering a total distance of 47,806 miles; this compares with 44,246 miles recorded in the previous six years.

'BULLETIN' NO. 8.

Here Dr. Lucas, assisted by Mr. MacNae, describes the distribution of the diatoms, those single-celled plants of many species which occur in enormous numbers, and make up a large proportion of the phytoplankton, the floating, microscopic vegetation, which forms the marine pastures upon which almost all the animal life of the sea ultimately depends for food. In the plates of Volume I, illustrating the distribution of the different organisms in the preliminary survey, the varying quantities found along the recorder lines were shown as graphs; in the present work, where there are so many intersecting lines across the area, such a method becomes impossible, and the relative values are shown as a series of numbers and other symbols representing the average quantities per mile for each consecutive ten-mile section of a record. In Text-fig. 1 a comparison is made between the old and new methods which will enable the results of this 1938–39 survey, as shown in the plates, to be more readily considered in relation to those obtained in 1932–37. As in the former survey, special attention has been given to the distribution of the diatoms *Rhizosolenia styliformis* and *Biddulphia sinensis*, which both may form dense concentrations in the southern North Sea in the autumn and are thought to be of particular importance in relation to the herring fisheries. Many more species have been dealt with in this survey than in the previous one, and Plates VIII to XXXVIII show the changing monthly patterns of distribution of some twenty different forms. This survey gives new evidence on the patchy nature of the diatom distribution and of possible water movements in the area. The principle contribution which this 'Bulletin' makes to our knowledge of the North Sea plankton is the presentation for the first time of many of the changes in diatom distribution month by month over the whole area for a twenty-month period; compared with an occasional survey of the area it has something of the quality of a moving or cinematograph picture compared with that of a still photograph. This and the other similar 'Bulletins' in this volume dealing with different groups of organisms are essentially studies of the ways in which the plankton distribution *changes;* they are specially designed to show movements with the passage of time. Each chart by itself is of little value compared with the consideration of a number of such charts in sequence. It is with the continued study of these changes, together with the changes recorded in meteorology, hydrology and in the fisheries, that we hope eventually to make a contribution towards a better understanding of cause and effect in the sea.

‘BULLETIN’ No. 9.

In this ‘Bulletin’ Dr. Lucas describes the distribution of those other important elements of the phytoplankton, the dinoflagellates and Phaeocystis; examples of these forms, together with the principal diatom species, are described and illustrated in the first explanation (see Text-fig. 12 on page xxv of Volume I). In the 1932–37 survey of the southern North Sea it was only possible to describe the detailed distribution of two different species of dinoflagellates—*Ceratium furca* and *C. fusus*; in the present ‘Bulletin’ for 1938–39 the monthly distribution of five other species in addition to these two is given for the whole North Sea area—*Ceratium lineatum*, *C. tripos*, *C. macroceros*, *C. horridum*, and *C. longipes*. As in the former ‘Bulletin’ for the diatoms these give us new knowledge of the actual *changing* distribution of plankton with the passage of time over a period of twenty months and over a wide area. Here too there is much interesting evidence on patchiness and of possible water movements. A striking feature of the distribution of the dinoflagellates as a whole, which is brought out in this survey, is the relative abundance found in the north-west and south-east corners of the area, and the comparative scarcity in the central region; this is well shown in Text-fig. 1 on p. 50.

‘BULLETIN’ No. 10.

Here are described the results of the first six recorder runs taken in the Atlantic on a line from the North of Scotland across the southern entrance to the Faeroe-Shetland Channel and out beyond the edge of the Faeroe Bank towards Iceland. This was a new venture begun in April, 1939, just before the outbreak of war. Phyto- and zooplankton are dealt with together. It represents a pioneer attempt to provide information to enable one to compare planktonic conditions in the North Sea with those further back in the Atlantic stream to the westward; this series of records, cut short by the war, is of course too small to form the basis for any definite conclusions. The interest of these data, however, will be increased when they can be compared with similar Atlantic records which have been taken since the war and will be described in subsequent ‘Bulletins’; they are published here as records of more value for the future than the present.

‘BULLETIN’ No. 11.

Here Mr. Rae and Mr. (now Dr.) Rees deal with the copepods, those small crustacea which as a group are consistently the commonest forms in the zooplankton. Illustrations of a number of different species will be found in Text-fig. 13 on page xxxvii of the Explanation to Volume I. At certain times, in restricted localities, the larvae of some other animal may outnumber them in the plankton for a period, but throughout the year they are the most abundant single type, and because of their numbers alone they play a vital part in converting the plants to animal protein. Relatively speaking, the copepod community is at low ebb during the winter in the North Sea, but in the spring, some time in April or May, they begin to multiply enormously. The authors show that there are several centres from which this rapid increase in the population starts and that one or two commoner species are responsible for their rapid build-up. Indeed, some of the less common species may be most numerous in the autumn or even during the winter months. The less common or less abundant species are not without interest, however, because they show well-defined limits of distribution and so may have value as *indicators* of water or, more important, of the movement of unusual environmental conditions. Four types of distribution are described in this 'Bulletin.' First, *Corycaeus* is restricted to an inshore band along the continental coast, rarely stretching far into the North Sea. Secondly, two species, *Labidocera* and *Isias*, are found only in the centre of the area concentrated over the Dogger Bank. Thirdly, *Euchaeta norvegica* and *Calanus hyperboreus* only appear over the Norwegian Deep. Fourthly, two species, about which we shall hear more, are found in the north-western part of the area where one might expect Atlantic conditions to impinge on those of the North Sea ; they are *Metridia lucens* and *Candacia armata.* Particularly interesting is the fact that the south-eastern boundary of the distribution of these two forms appears to move progressively into the North Sea month by month from July or August until the end of the year. Between 1932 and 1937, when our most northerly route was that running between Hull and Copenhagen, odd specimens of both *Metridia* and *Candacia* were taken each year off the Humber or over the Dogger Bank during the winter months, and they now appear to have been those which have gone furthest in their annual north to south progression, or of their penetration into the North Sea.

'BULLETIN' NO. 12.

As we said above (for 'Bulletin' No. 8), two species of diatoms hold particular interest, *Rhizosolenia styliformis* and *Biddulphia sinensis,* and warrant special attention. Dr. Lucas and Dr. Stubbings measured large numbers of individual cells to see what type of variation in size might be expected, and whether it was possible to detect different strains by this method. They found that in the 20 months for which they had samples of *Rhizosolenia* from the North Sea, those found off the Scottish coast in the influence of the Atlantic water were only about half the diameter of those in the southern part of the area, and on their size alone could be recognized as having a northern origin. In the case of *Biddulphia* the larger cells were to be found close to the shore in the Heligoland Bight and the size range decreased as one sampled further towards the centre of the North Sea, i.e., the Dogger Bank region.

Possibly we should explain here something about why the size, the diameter in particular, of a diatom may be of considerable significance. Each diatom is a single vegetable cell contained in a rigid shell made largely of silica. In principle, this shell comprises two halves, the one slipped inside the other like the two halves of a pill-box. When a cell divides, the two halves separate and each grows a new half pill-box inside itself; the outcome of this division is two daughter-cells, one identical in size to the former one, and the other fractionally smaller because it has grown a new half shell *inside* the smaller half of the old one.

The multiplication of the diatom crop at the time of the spring and autumn outburst is caused almost entirely by a rapid series of such cell divisions, some cells dividing into two as frequently as every few hours, but at each division half the daughter-cells are a little smaller than their parent so that gradually the average diameter of the population is reduced. Clearly such a procedure cannot go on indefinitely, and every so often, by a different mechanism of reproduction, a new population of large cells is formed. By measuring cells from samples taken each year from 1932 to 1939 and by combining these measurements with results of other workers, the authors are able to show in a most convincing manner the steady reduction in the average size of the cells and the sudden recovery at the time of spore formation. It appears that it takes something like three years for the cell diameter to drop from about 1/300 of an inch to 1/600th. This may at first seem to be a point of very little importance, but it may not prove to be so in the long run. If we could next determine accurately enough just how much a cell dropped in size at each division, we would have a type of estimate of how many cell divisions there had been in a given time or, indeed, how much plant life had been made available for the animal community. This might possibly, with much further work, be one of the ways of estimating productivity in the sea.

‘BULLETIN’ No. 13.

In this Mr. Marshall deals with the distribution of the forms of zooplankton other than the copepods and the young fish. His results confirm and amplify the ideas of geographic communities and boundaries of distribution outlined for the phytoplankton (‘ Bulletins’ 8 and 9) and the copepods (‘ Bulletin ’ 11); the weight of this confirmation is considerable, particularly for the north western community (see page 191). Not only does he find five or six animals of very different types behaving almost exactly in the same way as the two species of copepods, but amongst these is a species of arrow-worm, *Sagitta elegans*, which previous workers have demonstrated to be a typical inhabitant of the mixed Atlantic and North Sea water usually found at the north-western entrance to the North Sea and also of similar conditions in the English Channel. Another species of arrow-worm, *Sagitta setosa*, he found over the central North Sea, together with other characteristic forms, and the boundary between the two species of Sagitta moves south-east and north-west as the Atlantic flow into the North Sea waxes and wanes.

In another part of his ‘ Bulletin ’ Marshall compares the occurrence of the larvae of certain bottom-living forms, which are important in the diet of demersal fish in the plankton, with the previous surveys of the distribution of the adults on the North Sea bed. This work has been continued in greater detail and will be reported in future 'Bulletins.'

'BULLETIN' No. 14.

Here we consider in greater detail a single species of copepod during the 1938–39 period of the survey. Dr. Rees selected *Calanus* for his studies for a number of reasons; it had already been studied more than most species; it was sufficiently abundant to be of undoubted importance in the plankton complex, and it had a direct significance in being the staple diet of the herring. He shows that there are differences in the abundance and behaviour of *Calanus* in various parts of the North Sea and that, by and large, we may expect everywhere four periods of breeding or four generations in each year. Of these, the second, which takes place in April or May, is far and away the most successful.

For many years there has been discussion and argument between those concerned as to whether there were two recognizably *different* types of *Calanus finmarchicus* in the North Sea. On the one hand it was argued that there was another species called *Calanus helgolandicus,* and on the other that this form was indistinguishable from *Calanus finmarchicus.* That there is a recognizable difference between the two Rees has put beyond doubt by pointing out a consistent variation in the shape of one of the pairs of legs. Using this difference he is also able to show that one form is centred in the north and the other towards the south of the area.

'BULLETIN' No. 15.

A series of charts show the distribution of young fish and fish eggs during the 1938 and 1939 survey and also for the earlier years, 1932 to 1937. Unfortunately Dr. Stubbings left the staff before his account of this interesting side of the work was completed, so the consideration of these results must await a subsequent 'Bulletin' (No. 24 in Vol. III).

'BULLETIN' No. 16.

The small plankton-collecting device known as the Plankton Indicator and its use in herring research have been described in the Explanation to Volume I. The comparison between herring catches and the plankton found in the immediate vicinity has been continued but some modifications of the Indicator have been introduced. In this last 'Bulletin' of the volume, Dr. Barnes (of the Scottish Marine Biological Association) makes an experimental and statistical study of the reliability of the results obtained with the two models and compares their catching power and filtering efficiency. This highly technical paper is an important contribution to the herring-plankton work to be described later in that it establishes the validity of the method of sampling upon which so much of this work is based.

[*Hull Bulletins of Marine Ecology, No. 7, Vol. II, pp. 1–17, Plates I–V, September, 1941.*]

CONTINUOUS PLANKTON RECORDS:

GENERAL INTRODUCTION TO THE 1938–39 SURVEY

BY

A. C. HARDY, M.A., D.Sc., F.R.S.

The reports on the plankton recorder survey published in Volume I of the 'Hull Bulletins of Marine Ecology' dealt with the pioneer period, 1932–37, when the work was confined to the southern North Sea. Throughout this period it was our hope that this experiment in the new method should be the prelude to a wider ecological study of the plankton of the whole of the North Sea. In 1938 that hope was realized by the establishment of a new laboratory at Leith and the addition of new recorder lines between that port and Hamburg, the Skagerrak and the Shetlands, and from the Pentland Firth to Norway and to Hamburg. Another new line, between Hull and Norway, was also started in the spring of 1938, but was given up later in the year so that the equipment could be used to enlarge the area still further by recordings in the North Atlantic on a line towards Iceland across the southern entrance to the Faroe–Shetland Channel. This latest line, designed to link the changes in the North Sea with those in the North Atlantic current, was begun in April, 1939. Five months later, at the end of August, the war brought about a suspension of the whole programme.

There will be no need to stress the misfortune of this break in the continuity of our records, a continuity which is so important in all such ecological work.[1] Perhaps we may regard ourselves as fortunate in that we were able to complete twenty months of the extended survey before war came ; we have gained sufficient data to form an estimate of its value and to enable us to plan improvements in its design for the future. In addition to providing a picture of the main changes in the plankton over the larger area, the increased number of lines, which cross one another at so many points, enable one to form a better idea of the size and shape of the denser concentrations of different organisms than was possible before. The crossing lines at their points of intersection provide on the whole important confirmatory evidence, and the degree of agreement usually found on the intersecting records has given added confidence in the method. It has been possible during this period to increase the number of specific identifications made in the routine analyses, and so provide a larger number of organisms which may be considered as indicators in the interpretation of the main water movements in the area.

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[1] It is gratifying that, in spite of the war, the method is being carried on, and we hope further developed, in other parts of the world. During last year (1940) the Department supplied a recorder and equipment to the Government of Australia for use in their fishery investigations, and two recorders and equipment were sent on loan to the Wood's Hole Oceanographic Institution, U.S.A., for use in a survey off the east coast of America.

This brief account of the organization of the extended survey will form an introduction to the papers which will follow dealing with the results obtained up to the outbreak of war. For a full discussion of the aims and scope of this work, and the limitations to the method, 'Bulletin' No. 1 should be consulted. The reports to be published immediately will be essentially factual, setting out, mainly in graphical form, the monthly changes in the distribution of the more important plankton species over the area. These, together with the 1932–37 reports, will then form the basis for subsequent papers devoted to a more general discussion of the ecological problems involved.

As already explained in Bulletin I the extended survey was planned by the Joint Advisory Board,[1] set up at the invitation of the College, on which I was joined by Dr. E. S. Russell, O.B.E., Director of Fisheries Investigations, Ministry of Agriculture and Fisheries, and Dr. R. S. Clark, Scientific Superintendent to the Fisheries Division, Scottish Home Department (late Fishery Board for Scotland). A close co-operation and exchange of results with the two government departments has been maintained throughout the course of the investigations. The realization of the plan was made possible by increased grants provided by His Majesty's Treasury on the recommendation of the Development Commission and by the Council of the University College of Hull.

For the new laboratory at Leith we were fortunate in being able to obtain the lease of most convenient premises, consisting of a set of large first-floor rooms situated close to the entrance to the docks.[2] Two front rooms, equipped as laboratories, are excellent for microscopic work, since they are well lit by large windows facing towards the north and overlooking an open square. Another room was furnished as a preparation room and workshop for the reconditioning of the recorders; this we provided with a hoist and a trapdoor in the floor, so that the recorders could be lowered and raised to and from the entrance hall below, where a trolley was kept to convey the machines to the ships.

Mr. C. E. Lucas, who joined our staff at the beginning of our plankton investigations in 1931, was appointed to be in charge of this new station, with Mr. N. B. Marshall and Mr. C. B. Rees to assist him. In a remarkably short time the laboratory began to have the appearance of a well-established department. At our Hull headquarters my staff consisted of Dr. G. T. D. Henderson Mr. K. M. Rae and Mr. W. Macnae, who, on leaving to take up other work in September, 1939, was succeeded by Dr. H. G. Stubbings. The successful operation of this extended survey is due to the excellent team work of these two research groups. The three members of staff at each station continued the system of specialization which had been adopted in 1936 ; the records were first examined by the phytoplankton specialists, then by the experts on the Copepoda, and finally by those concerned with the remainder of the zooplankton (C. E. Lucas, C. B. Rees and N. B. Marshall respectively at Leith, and W. Macnae, K. M. Rae and G. T. D. Henderson[1] respectively at Hull). Dr. Stubbings took over a study of the young fish and fish-egg material for the present and past surveys from Dr. Henderson, who was called to service in the R.N.V.R.

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[1] See also the preface to Vol. I.

[2] At the corner of Sandport and Commercial Streets (address: Oceanographic Laboratory, 23, Sandport Street, Leith, Edinburgh 6).

Our debt of gratitude to the many different people who have helped in the work has been acknowledged in a special section of 'Bulletin' No. I (Vol. 1, p. 53), but it should again be emphasized that the very existence of the survey depends upon the kind interest taken in it by the directors of the different companies which have co-operated in the scheme, and in the ever ready help so willingly given by their shore staffs and by the captains, officers and crews of the ships concerned.

The methods used at sea and in the laboratory have been fully described in 'Bulletin' No. 1 except for certain details of laboratory technique involved in the specialized treatment of the different groups, which will be described in the appropriate papers which follow. Throughout the 1938–39 survey the recorder rolls were analysed, as at the end of the 1932–37 survey, in consecutive units or "blocks" each representing a distance of 10 miles. It should be kept in mind that the essence of the method is that of a continuous sampling ; the consecutive ten mile blocks should not be considered as a series of separate collections made at ten-mile intervals, for each is a sample taken along a ten-mile stretch.

The same ten-mile blocks, always measured from the normal beginning of a line (a particular light-vessel or lighthouse), are maintained throughout the survey ; *i. e.* should the record begin, say, at six miles past the normal starting point, the blocks will be measured, not from the *actual* start of the record, but from the *normal starting point.* In the example just given the first block would be short, only representing a distance of four miles, and would be rejected as being of less than half the block. Similarly there may be a block at the end of the record which may represent less than ten miles and, if less than five miles, would again be rejected. A reference, say, to blocks 9 and 14 on *any* record will refer respectively to sections representing the parts of the line which lie between 80 and 90 miles, and between 130 and 140 miles from the normal starting points ; for any particular line they will *always* refer to the same stretch of the North Sea.

In the subsequent papers it will be seen that a change has been necessary in the graphical presentation of the results. With so many intersecting lines it has been impossible to continue the method of showing the varying abundance of the different species as continuous graphs, since the confusion due to overlapping was too great ; instead, either a series of symbols representing ranges of numerical values, or numerical values themselves, or both, have been employed.

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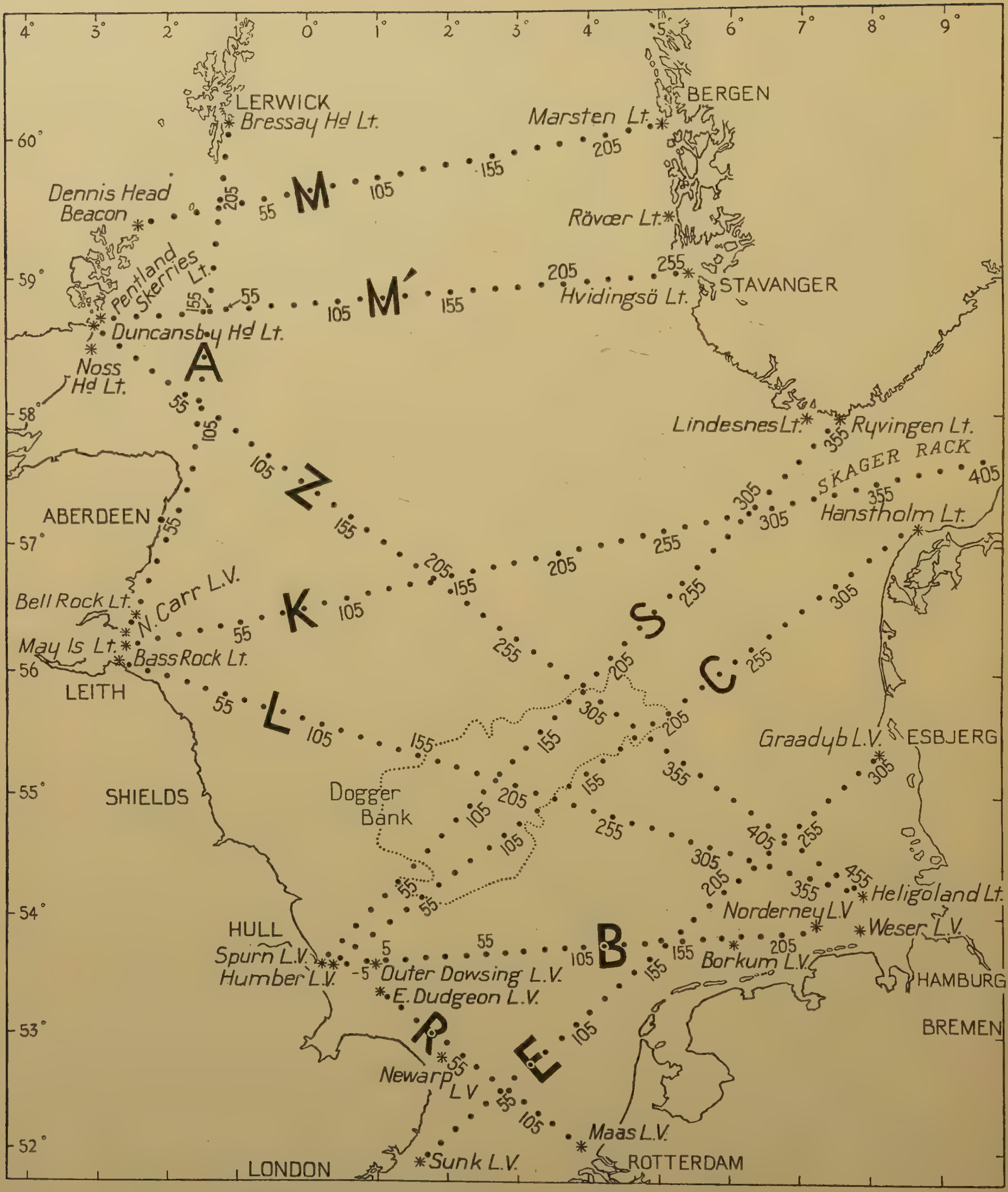
[1] The Chaetognatha and Euphausiacea from Hull were sent for identification to Mr. Marshall, who has specialized on these groups.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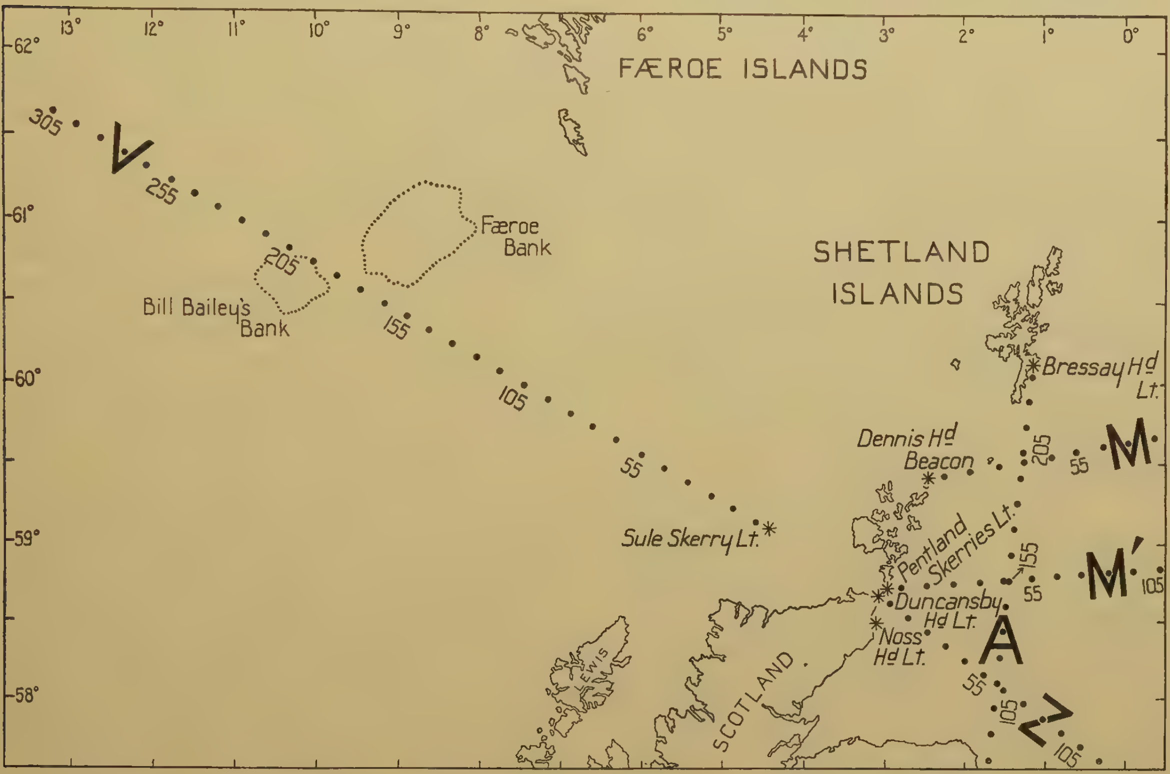
Dennis Head Beacon
M
Rövær Lt.
Pentland Skerries Lt.
M′
Hvidingsö Lt.
STAVANGER
Duncansby Hd Lt.
Noss Hd Lt.
A
Lindesnes Lt.
Ryvingen Lt.
SKAGER RACK
Hanstholm Lt.
Z
ABERDEEN
Bell Rock Lt.
N. Carr L.V.
K
S
May Is Lt.
Bass Rock Lt.
LEITH
C
L
Graadyb L.V.
ESBJERG
SHIELDS
Dogger Bank
Heligoland Lt.
Norderney L.V.
Weser L.V.
HULL
Spurn L.V.
Humber L.V.
Outer Dowsing L.V.
B
Borkum L.V.
HAMBURG
E. Dudgeon L.V.
BREMEN
R
E
Newarp L.V.
Maas L.V.
ROTTERDAM
LONDON
Sunk L.V.

TEXT-FIG. 1.—Chart showing the recorder lines of the 1938–39 plankton survey of the North Sea. The distances along the lines from the usual starting-points (light-vessels or lighthouses) are shown in miles. The black dots are at 10-mile intervals representing distances of 5, 10, 25 . . . miles from the start and marking the mid points of the standard "10-mile blocks" used in the analysis of the records. The course of the "V" line in the North Atlantic is shown in Text-fig. 2.

The different recorder lines have been given reference letters, A, B, C, etc., to distinguish them, and each separate record on each line has a serial number, A1, A2, A3, etc. The approximate course of each line is shown in Text-figs. 1 and 2. The dots along each line represent the middle point of each "ten-mile block" used as the unit of analysis; they therefore represent distances of 5, 15, 25 . . . miles from the light-vessel or lighthouse marking the normal beginning of the record. On some occasions the line deviated from the normal course; sometimes the recorder was shot late or hauled up early on account of fog, heavy weather, or the presence of herring drifters with their nets out, or again a record may have been cut short by a mechanical failure in the recorder. In some months a record may have been missed altogether, either through a ship being taken off service, through stress of weather, a shortage of machines or on account of a complete failure of the mechanism. The track and extent of each record, together with its date, times and position of its start and end, are shown month by month in Plates I to V. It should be realized that the actual course of the ship may be ten or even more miles to right or left of the track shown on the chart. A discussion on the possible errors in


13°
12°
11°
10°
9°
8°
6°
5°
4°
3°
2°
1°
0°
62°
61°
60°
59°
58°
FÆROE ISLANDS
V
305
255
205
155
105
55
Færoe Bank
Bill Bailey's Bank
SHETLAND ISLANDS
Bressay Hd Lt.
Dennis Hd Beacon
205
55
M
Sule Skerry Lt.
Pentland Skerries Lt.
155
55
M'
105
Duncansby Hd Lt.
Noss Hd Lt.
A
55
105
Z
105
LEWIS
SCOTLAND

TEXT-FIG. 2.—Chart showing the course of the "V" line across the entrance to the Faroe–Shetland Channel and its spatial relation to the A, M and Z lines of the North Sea survey. The black dots have the significance explained in Text-fig. 1.

positions in mid-course through the effect of sea and tide will be found in ‘ Bulletin ’ No. 1 (Vol. I, p. 39).

As in the 1932–37 survey, each recorder was run at a standard depth of 10 metres below the surface. Diagrammatic vertical sections along the A, K, L, M, S and Z lines are given in Text-fig. 3 to show the variations in the depth of the sea along these routes. Similar diagrams for lines B, C, E and R will be found in ‘ Bulletin ’ No. 1 (Vol. I, p. 49). The diagram for line V will appear in a subsequent paper devoted to the results of this line across the Faroe–Shetland channel.

The depths in the northern area are very much greater than those in the south, and consequently we may expect the variations in the vertical distribution of the plankton, particularly those due to the diurnal vertical migrations of some members of the zooplankton, to have a more marked effect upon our results in the north than they do in the south. Due attention is being given to this in the subsequent papers. That part of each record taken during the hours of darkness (between sunset and sunrise) is shown in Plates I–V as a thicker line than the part taken in daylight.

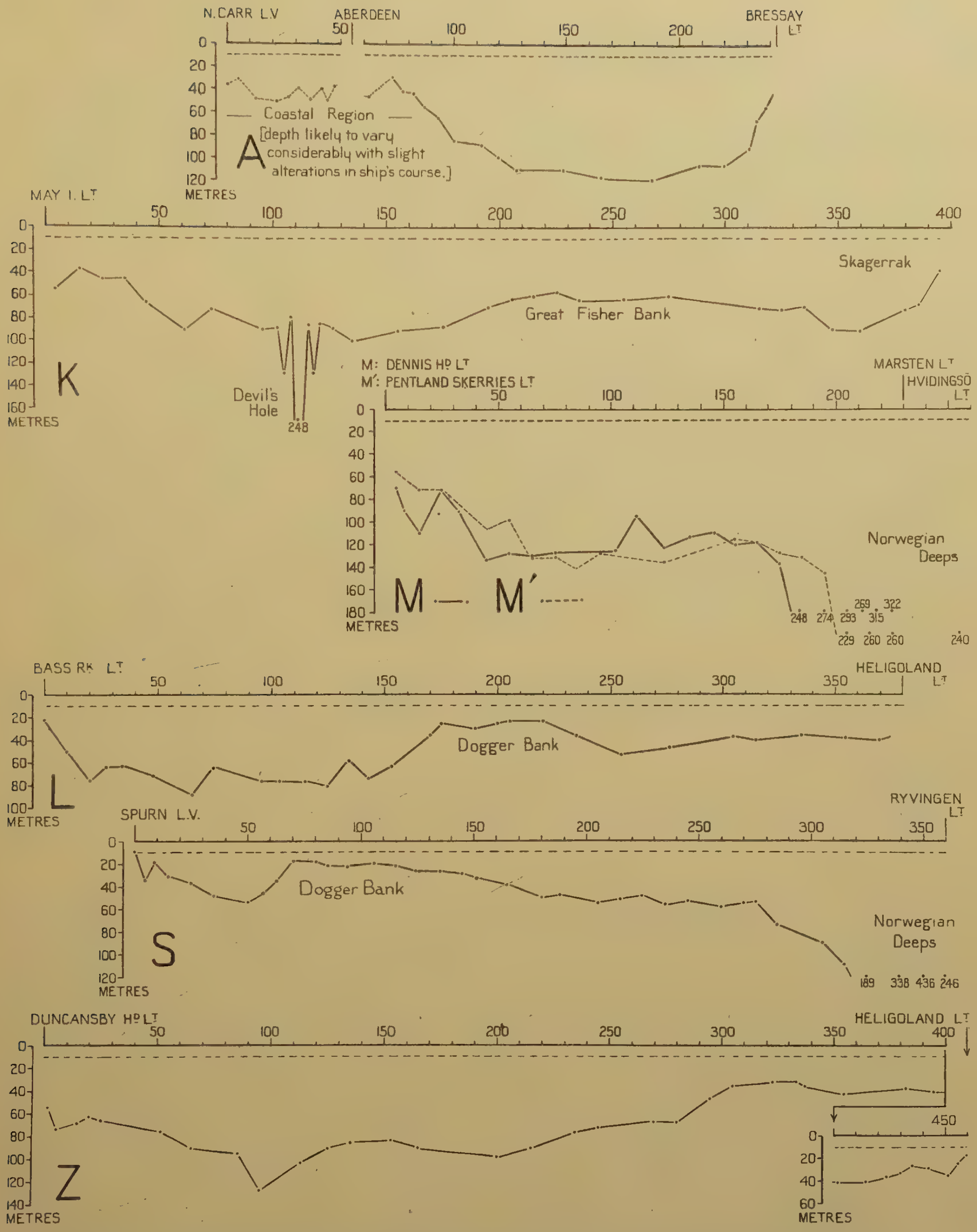
As far as possible an attempt was made to run the different recorder lines as nearly together in time as possible ; this was the ideal aimed at, but in practice, again through such various causes as stress of weather, alterations in ships’ sailing schedules, or sometimes through shortage of machines, it was far from being achieved. The dates of the records are shown on the margin of the maps in the plates.

Details of the mileage covered on each record, together with observations on the wind, sea and weather as reported by the ships’ officers on the log forms provided, are given in the summary list appended. During the 20 months of the 1938–39 survey 188 records were obtained, covering a total distance of 47,806 miles, making a grand total of 92,052 miles since the survey began in 1932.

Each recorder line will now be described in turn in alphabetical order.

The A Line.

On this line the recorder was run on the S.S. *St. Sunniva* of the North of Scotland and Orkney and Shetland Steam Navigation Co. between Leith and Lerwick, calling at Aberdeen on the way. This ship only runs for part of the year, from the end of April to early November ; but this is the important period for obtaining correlations between the plankton and the results of the Shetland, Orkney and East Scottish herring fisheries. The recorder was put down on passing the North Carr Light-vessel, hauled up on approaching Aberdeen, put down again on leaving that port, and finally hauled up on reaching the Bressay Head Lighthouse before going into Lerwick. The course is described in the outward direction, but more often than not the recorder was used between these points on the return journey. Positions on the line are measured in miles from the North Carr light-vessel. The actual distance along the course from the North Carr Light-vessel to



TEXT-FIG. 3.—Diagrams representing vertical sections through the sea along the A, K, L, M, S and Z lines. The vertical scale (in metres) is greatly exaggerated. The surface of the sea is shown as the line of the horizontal distance scale (in miles), the path of the recorder as a broken line, and the sea-bed by lines connecting points representing soundings along the routes taken by the ships. Diagrams for lines B, C, E and R were given in Text-fig. 29 of Hull 'Bulletin' No. 1 (Vol. I, p. 49).

the Bressay Head Light is 234 miles, whereas the total distance given for a complete record is only 229 miles; this discrepancy is explained by the gap in the record between entering and leaving the port of Aberdeen. The line was begun on 3rd May, 1938, and because of its importance in relation to the herring fisheries it was run as far as possible twice each month throughout the summer.

THE B LINE.

This is one of the original lines of the southern North Sea 1932–37 survey, run between Hull and Bremen or Hamburg, on ships of a German line—the Argo Shipping Company. It was formerly run on the S.S. *Albatross*, but latterly on the S.Ss. *Geier* and *Habicht*, which took over the service after the withdrawal of the *Albatross*. In the early days of the survey the recorder was put down at the Outer Dowsing Light-vessel and taken up at the Borkum Light-vessel or *vice versa*, but in 1937 the line was extended from near the Humber Light-vessel at the English end and to the Norderney Light-vessel off the German coast. For convenience of comparison with former records we have continued to refer to positions on the line in miles measured from the Outer Dowsing Light-vessel; positions on the short stretch of the line to the west of this light-vessel are expressed as minus quantities, *e.g.* −21, −24, etc., as shown for January, February, etc., on Plates I–V. This, actually the first line to be run, has always been regarded as one of the key lines passing through the centre of the southern North Sea area; it is particularly unfortunate that we experienced some long gaps in our records on this line during 1938–39 due to the ships, with their equipment, being transferred unexpectedly to other services.

THE C LINE.

This is another of the original lines of the southern North Sea 1932–37 survey, run between Hull and the Skagerrak, on the S.S. *Spero* of the Ellerman's Wilson Line sailing to Copenhagen. The recorder is put down at the Humber Light-vessel and taken up opposite the Hanstholm Lighthouse at the entrance to the Skagerrak (up to the middle of 1937 it had only been run for a distance of 250 miles towards the Skagerrak). As the ship passes over the south-west patch of the Dogger Bank the recorder is hauled up to 8 metres' depth for a short period and then lowered again to the standard 10 metres; this is a safety measure to avoid the risk of hitting the bottom in a heavy swell.

THE E LINE.

This line was introduced in 1936, using the ships of the Danish line, the United Shipping Company, sailing between London and Esbjerg, formerly the S.S. *Frigga*, but latterly the S.S. *Vidar*. The recorder was run between the Sunk Light-vessel, off the Essex coast, and the Graadyb Light-vessel on the approach to Esbjerg.

During the course of the survey the Sunk Light-vessel was moved two miles to the south-west of its former position. In order to have continuity of reference between similar sections of the line, before and after the change, all points on the line are still referred to in terms of miles distance from the light-vessel's old position. The recorder is still usually put down or taken up as the ship passes the Sunk Light-vessel so that the position of the western end of such a record is now referred to as -2 (*i. e.* two miles to the south-west of the old position of the Sunk Light-vessel).

The K Line.

Started in January, 1938, this is one of the new lines of the northern area, running between Leith and the Skagerrak on the S.S. *Hengist*, of Messrs. James Currie & Co., sailing to Copenhagen. The recorder is put down on passing the May Island Lighthouse and taken up in the Skagerrak after being towed a distance of about 400 miles towards the Skaw Lighthouse, or it may be run in the reverse direction. Positions on the line are measured in miles from May Island. On two occasions (charts June and July, Plate II) the ship made for the Lindesnes light in Norway, and the recorder was taken up before reaching or when passing that point.

The L Line.

Another new line, begun in February, 1938, is run between Leith and Hamburg on the S.S. *Gothland*, also a ship of Messrs. James Currie & Co. On the outward voyage the ships often called at Dundee before sailing for Hamburg, when the recorder was run from the Bell Rock Lighthouse, instead of the Bass Rock, to the Heligoland light. The alternative courses lie very close to one another.

The M Line.

This is a line of great importance between the North of Scotland and Norway cutting across the Atlantic influx into the Northern entrance to the North Sea. It was run on the S.S. *Cygnus* of the Norwegian line Det Bergenske Dampskibs-selskab which sailed between Bergen and the ports of Manchester and Glasgow *via* the north of Scotland. The recorder was loaded on the ship at Manchester, but was not used until the ship began her passage across the North Sea. Her course, as will be seen from the charts in Plates I–V, varied considerably; usually she passed through the Pentland Firth, but on many occasions she would pass to the north of the Orkneys. Sometimes she would make direct for Bergen, but at others she would make for some other point on the Norwegian coast, as far south as Stavanger and pass north to Bergen along the coast. The two principal courses are shown in Text-fig. 1 as M and M′ and the various deviations in the different months are recorded in the plates. On the more northern course the positions are measured off in miles from the Dennis Head Beacon, and on the southern and more usual course, from the Pentland Skerries light; at these points the recorder was put down or taken up on the outward or return voyages. On the Norwegian side the recorder was taken up at a variety of points the ship made for, such as the Hvidingsö, Rövoer or Marsten Lighthouses. The distance across the northern entrance to the North Sea is only some 250 miles, so that by supplying the recorder with an extra long roll of gauze to cover a total distance of just over 500 miles we were able to obtain a record both on the outward and return journey. By providing the officer in charge with an indelible ink pencil on the end of a stick he was able to make a mark on the gauze by inserting the pencil and stick through the front aperture of the machine ; in this way we could determine the point on the roll which marked the end of the passage to Norway, and the beginning of the return record. In December, 1938, the ship made a return voyage *via* Newcastle and took a record as shown in Plate III.

THE R LINE.

This is another of the original lines of the southern North Sea survey begun in June, 1932, and run on the ships of the Associated Humber Lines. During 1938–39 the ship was the S.S. *Dewsbury*. The recorder is put down at the East Dudgeon Light-vessel and taken up at the Maas Light-vessel, or *vice versa*. On the charts the course is shown as a straight line between these two points, but actually it deviates slightly from this line to pass close to the Newarp Light-vessel. Positions on the line are marked off as distances from the East Dudgeon Light-vessel. It is a particularly important line cutting across the southern entrance to the North Sea from the Channel.

THE S LINE.

Begun in February, 1938, on the S.S. *Salerno* of the Ellerman's Wilson Line, this line ran between Hull and Norway. When it was planned the ship was in service on a direct passage between Hull and Stavanger, a course which would have given a very valuable record across the centre of the North Sea ; actually no sooner had the equipment been fitted to the ship than altering trade conditions made her sail either for Christiansund or Oslo. This new course lay too near to that of the C line to be really worth while ; with only a limited amount of equipment available it was decided to abandon it at the end of August. The equipment was transferred to the V line begun in the following year. The recorder was put down on passing the Spurn Light-vessel and taken up at a point off the Norwegian coast—usually the Lindesnes or Ryvingen Lighthouses. Positions on the line are referred to in miles from the Spurn Light-vessel.

THE V LINE

This, perhaps the most interesting line of the survey, was only begun in April, 1939, on the S.S. *Gullfoss*, of the Icelandic Shipping Company, sailing between Leith and Iceland. From the Pentland Firth the ship makes a course for the Westmann Islands, crossing the southern end of the Faroe-Shetland Channel, and so across the North Atlantic current, a branch of which eventually passes round the north of the Shetland Isles and into the North Sea. The recorder was put down on passing the lighthouse on Sule Skerry and towed for 300 miles, a distance that carries it across the entrance to the channel and well beyond the Faroe Bank. We obtained six runs from April up to the outbreak of war, giving interesting records of "indicator" species which will be the subject of a special paper to follow. Had we been able to continue this line, it should have provided a most important link between the changes in the north Atlantic current and subsequent events in the North Sea. It is hoped that it may be resumed with more Atlantic lines after the war. Its course in relation to the northern North Sea lines is shown in Text-fig. 2. Positions on the line are measured from the Sule Skerry light.

The Z Line.

Begun in February, 1938, this line runs from the Pentland Firth to Hamburg on ships of Messrs. James Currie & Co. (S.Ss. *Zealand*, *Lapland* and *Courland*) sailing from Glasgow round the north of Scotland. The recorder was loaded at Glasgow, but not put down till leaving the Pentland Firth. At first it was run for the full distance from Duncansby Head to the Heligoland light, but later the length of tow was cut down to be not more than 400 miles to avoid strain on the towing cable.[1] Part of the line was eliminated at each end since these two areas were served by other lines : M and A in the north, and L in the south. Positions on the line were measured from the Duncansby Head light. On occasions the line ran on a course between the Noss Head Lighthouse and the Weser Lightship—a course very close and parallel to the more usual one. In July, 1939, the ship called at Lerwick on her way to Hamburg and took a record as shown in Plate V.

Full details of the records will be found either in the summary list or in the Plates (I–V). The former gives the date, mileage recorded, miles per section, observations on the wind, sea and weather provided by the ships' officers, and remarks regarding any defects or a particular feature of the record (see explanation of the summary list below), while the Plates give the line and direction of tow of each record, position, date and times of its beginning and ending, and the parts of each record run during hours of darkness (see explanation of Plates).

Explanation of Summary List.

Route and Number of Record.

The routes described above are arranged in alphabetical order and the records on each route in chronological sequence. When a record number and its details are omitted it indicates that no useful record was obtained, either on account of a mechanical failure at the very beginning of the run or through an accident to the recorder.

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[1] See Bulletin ' No. 1 (Vol. I, p. 31).

Mileage Recorded.

When the recorder has not been towed the whole distance between two light-vessels the mileage given is that of the ship's automatic log (corrected when possible). Reference has already been made to the discussion in 'Bulletin' No. 1 (Vol. I, p. 39) on the possible errors in log estimations and their corrections. On occasions when there has been a mechanical defect resulting in a stoppage of the mechanism (marked " D " in the remarks column) the mileage recorded is estimated from the number of sections on the gauze which have been exposed before the stoppage, by taking a ratio of miles per section based on the past records of the machine concerned. In such cases the estimated mileage is only an approximation and is given as " *ca.* 140 " or " *ca.* 209 " (as in A1 or B115). The letter Q indicates a record or part of a record which may be of qualitative value only (see reference to " d " in the " Remarks " section below).

Miles per Section.

As explained in ' Bulletin ' No. 1, the gauze sampling the plankton is divided into numbered sections by transverse lines 2 in. apart. The miles per section represents the mileage travelled by the machine in the time taken for each dividing line in the gauze to pass across the water tunnel. It is obtained by dividing the mileage recorded by the number of sections of the gauze which have been exposed. Actually, as already explained, the 2-in. sections have not been used in the 1938–39 survey as the units of analysis, but instead sections have been cut off each, representing ten miles of sea traversed.

Wind, Sea and Weather.

The conditions of wind, sea and weather were recorded by the ships' officers on the log forms provided. The conditions of wind and sea, where not already given in numbers, have been converted into their appropriate numbers on the Beaufort Wind Scale and the Douglas Sea Scale, which are as follows :

Beaufort Wind Scale.		Douglas Sea Scale.	
0	Calm.	0	Calm.
1	Light air.	1	Smooth.
2	Light breeze.	2	Slight.
3	Gentle breeze.	3	Moderate.
4	Moderate breeze.	4	Rough.
5	Fresh breeze.	5	Very rough.
6	Strong breeze.	6	High.
7	Moderate gale.	7	Very high.
8	Fresh gale.	8	Precipitous.
9	Strong gale.	9	Confused.

Instructions are given to the officers in charge not to use the recorder in seas of over 6 in the Douglas scale. The following abbreviations have been used to indicate the state of the weather :

b.	blue sky.	o.	overcast.
bp.	bright periods.	p.	passing showers.
c.	cloudy.	q.	squalls.
cl.	clear.	r.	rain.
f.	fog.	s.	snow.
fn.	fine.	st.	storm.
h.	hail.	t.	thunder.
m.	mist.	z.	haze.

Remarks.

The following are the explanations of the reference letters used in the remarks column :

c : Machine still fitted with clutch drive mechanism, *i. e.* not yet fitted with the fusee improvement described in ‘ Bulletin ’ No. 1 (Vol. I, p. 24).

D : A mechanical defect resulting in a stoppage of the mechanism (see note above under “ *Mileage recorded* ”).

d : A slight mechanical defect, such as a crumpling of the silk, which, however, does not appreciably affect the ratio of miles per section, but may result in a record being of only qualitative value (marked Q in mileage recorded column).

P : Indicates that the record was analysed for phytoplankton only. At the time of the autumn East Anglian herring fishery a number of extra records have been taken from 1934 onwards to give a more detailed knowledge of the changes in the phytoplankton, and these usually have been analysed only for phytoplankton and young fish.

u : A few records for which the silk was still used in the unfolded condition (see ‘ Bulletin ’ No. 1, Vol. I, p. 26).

V : Indicates that the silk had over-wound due to an unexpectedly long tow. As in D, only an approximate ratio can be used.

Summary List of Records, 1938–39.

(See explanation on preceding pages.)

Route and number of record.	Date.	Mileage recorded.	Miles per section.	Wind.	Sea.	Weather.	Remarks (see p. 13).
	1938.						
A 1	3/4.v	*ca.* 140	*ca.* 5·0	E.N.E.–N., 4	3–2	fn. cl.	D, c
2	14/15.v	160	5·25	S	3	z.–f.	c
3	18/19.vi	229	5·00	S., 5–W., 2	3–2	o.–cl.	
4	2/3.vii	229	4·92	W.–S.W., 2	2–1	c.	c, u
5	16/17.vii	229	5·18	var., 1–2	1	o.	
7	13/14.viii	177	5·32	W., 2	1	fn., cl.	
8	27/28.viii	229	5·15	N.W., 2	1	,,	
9	10/11.ix	229	5·43	W., 5–2	4–2	o. r.	
10	1/2.x	229	5·69	S., 2–5	3	o. z.	
11	14/15.x	229	5·31	W., 6–5	6–2	cl. q	
12	4/5.xi	229	5·50	N.E.–S.W., 5	4	o. r.	
	1939.						
13	25/27.iv	233	4·15	N., 4–5	3	cl. p.	
14	12/13.v.	229	4·29	N.E., 2	1	c.	
15	27/28.v	229	4·60	S.S.W.–W., 2	1	o.	
16	10/11.vi	229	4·47	W.N.W., 4	3	o. p.	
17	17/18.vi	229	4·34	S., 5	4	z.	*
18	1/2.vii	229	4·79	W., 4	2	fn. cl.	
19	29/30.vii	229	4·95	S.S.W., 5–4	3–2	cl.	
20	12/13.viii	177	4·94	W., 2	1	fn. cl.	
	1938.						
B 115	26.i	*ca.* 209	*ca.* 4·75	W., 5–2	4	o. p. r.	D, u
116	23.ii	184	4·65	var., 1–2	2	fair	
117	8/9.vi	224	4·27	var., 1–2	2	,,	
118	6.vii	208	4·27	W., 2–3	0	,,	
119	9/10.viii	182	5·38	E., 2–3	3	—	
121	6/7.ix	246	5·18	N.W., 4	3	fair	P
122	20/21.ix	246	5·36	S., 5	4	—	
123	19/20.x	246	5·38	W., 7–N.W., 5	4	c. r.	
124	25/26.x	247 Q	5·26	N., 6–2	3	c.	d, P
125	2/3.xi	246	5·17	W., 5–6	4	,,	P
127	16/17.xi	251	5·36	E.S.E., 2	3	c. o. m.	
128	22/23.xi	119	5·10	S.S.W., 3–9	3–4	c. o. r.	P
129	30.xi/1.xii	247	5·11	S.W., 3–7–3	3–4	,,	P
130	14/15.xii	247	5·36	S.E., 4	3	c. o. m.	
	1939.						
131	20/21.i	206	5·05	S.E., 4–6	3	—	
132	17/18.ii	219	4·91	N.W.	4	—	
133	11.iii	194	5·43	S., 3–E.S.E., 4	2	fn. cl.	
134	8/9.vii	261	5·38	S.S.W., 1–7	—	r.	
	1938.						
C 66	19/20.ii	306	4·59	N.E.–N., 4	3–4	—	
67	5.iii	*ca.* 27	*ca.* 5·0	W.–W.N.W., 7	4–5	—	D
68	15/16.iv	*ca.* 277	*ca.* 5·0	N., 5–N.W., 7	5	—	D
69	14/15.v	110+223 Q	5·20	S., 2	2	fn. cl.	D
71	25/26.vi	308	4·21	W.–N.W., 6	4	—	
72	9/10.vii	307	5·03	N.W., 4–5	3–4	o. r.	
73	12/13.viii	350	5·12	var., 2	3	—	
74	3/4.ix	338	4·82	W., 4–N., 2	3	c. o. q. r.	

* Coarse silk (30 mesh to 1 in.) used for the capture of young fish.

Route and number of record.	Date.	Mileage recorded.	Miles per section.	Wind.	Sea.	Weather.	Remarks (see p. 13).
	1938.						
C 75	1/2.x	336	5·15	S.E.–E.S.E., 2	2	c.–cl. p.	
76	29/30.x	335	4·89	E.N.E.–E.S.E., 2	2	—	
77	26/27.xi	333	4·83	S.S.W.-W.N.W., 7	6	c.–cl.	
78	24/25.xii	334	5·29	E.N.E., 6–4	4·3	o. s.	
	1939.						
79	21/22.i	335	5·12	S.E., 4	3	o.	
80	18/19.ii	340	5·18	N.W.–N.N.W., 6	5	c.–cl.	
81	15/16.iv	336	5·04	W., 4–S.W., 5	3–4	fn. cl.	
82	13/14.v	341	4·97	N.E., 4	2–3	—	
83	10/11.vi	338	5·35	S.W.–W., 2	2	fn. cl.–c.	
84	8/9.vii	335	5·17	S.W., 5–6	3–4	c. r.	
85	19/20.viii	313	5·13	E.N.E., 2	2	h.–f.	
	1938.						
E 18	23/24.ii	277	4·99	2	2	fair	
20	10/11.v	279	4·65	S.E.–S., 3	3	c. cl.	
21	14/15.vi	241	4·99	N.W., 3–6	3–6	c. p.	
22	27/28.vii	304	5·31	S.W.–S.E., 3	2–3	b.	
23	24/25.viii	298	5·04	S.E.–N.E., 3	3	,,	
24	11/12.x	*ca.* 42	*ca.* 5·0	W., 4–S.W., 6	4–6	c. r.	D
25	16/17.xi	221	5·31	S.E., 2–S.S.E., 1	2–1	c.	d
26	13/15.xii	306	5·31	S.S.E., 3–S.E., 5	3–5	c. m.	
	1939.						
27	11/12.i	306	4·94	S., 4–3	4–3	c. p.	
28	7/8.ii	202	4·96	S.W., 3	3	c. f.	
29	21/22.iii	259	5·06	N.W., 2–S., 5	2–5	c. r.	
30	19/20.iv	300	5·26	N.W., 2	2	b.	
31	17/18.v	275	4·82	var. 3–1	3–1	r. c. f.	
32	14/15.vi	306	5·42	S.S.E.–S., 2	2	c. cl.	
33	18/20.vii	314	5·68	S.E., 3	3	c. r.	
34	15/17.viii	305	5·48	var., 2–1	2–1	cl. c.	
	1938.						
K 1	21/22.i	366	5·41	W., 7–S.W., 4	4	cl. b.	c
4	1/2.iv	355	5·03	W., 4–S.W., 7	3–5	—	c
5	29.iv	*ca.* 50 Q	*ca.* 5·0	N.E., 5–6	6	c. cl.	D
8(*a*)	1/2.vii	219	5·31	N.W., 5–W., 6	4	f.	
8(*b*)	8.vii	90	5·31	S.W., 5–6	4	cl.	
9(*a*)	29/30.vii	324	5·64	S.S.W., 5	3	o, p.	
9(*b*)	5.viii	91	5·64	E., 2	2	fn. cl.	
10	26/27.viii	370	5·30	N., 5–W., 6	2–4	b.–o.–c.	
11	23/24.ix	216+157 Q	5·74	S.E., 5–S.S.E., 6	2–4	c. z.	d
12	21/22.x	378	5·62	S., 2–S.S.E., 6	3	c. o. cl.	
13	18/19.xi	402	5·45	S.S.W., 5–W.S.W., 6	4–6	c. cl. p.	
14	23/24.xii	394	5·76	E.S.E., 4–5	3	o. c.	
	1939.						
16	26/28.i	331	5·47	N.E.	3–4	o. c.	
18	10/11.iii	370	6·44	N.E., 2–var.	2	c.–fn. cl.	
19	7/8.iv	388	4·82	S., 2–4	3	fn. cl.	
20	12/13.v	119+213 Q	4·96	N.E.	3	o.	d
21	25/27.v	402	5·07	S.E.	2–3	fn. cl.	
22	30.vi/1.vii	369	4·47	W.–N.W.	3–4	o. c.	
23	28/29.vii	349	4·83	W., 5–6	3	c. cl.	
24	18/19.viii	325	5·34	var., 2	1	fn. cl.	

Route and number of record.		Date.	Mileage recorded.	Miles per section.	Wind.	Sea.	Weather.	Remarks (see p. 13).
		1938.						
L	1	4/5.ii	328	4·64	S.W., 6	4	c. q.	c
	2	18.iii	32	5·57	S.W., 4–7	4–7	—	
	3	1/2.iv	351	5·01	W., 4–W.S.W., 7	4–8	—	
	4	13/14.v	378	4·74	S., 2–S.E., 3	2	c	
	5	11/12.vi	290	4·84	N., 3	2	,,	c, u
	6	15/17.vii	370	5·25	E.S.E., 2–S.W., 3	3–2	fn.	
	7	12/14.viii	321	5·20	N.E., 2	2	,,	
	8	20/22.ix	315	5·29	S., 3–S.W., 5	3–4	—	
	9	11/12.x	275	5·59	W.S.W., 5–S.W., 7	3–6	c. o.	
	10	3/4.xii	371	5·60	var., 1–3	3–2	c. cl.	
		1939.						
	11	5/6.i	326	5·43	N., 4–N.E., 3	3	c. cl.	
	12	4/5.ii	381	4·96	S.W., 5–W., 4	4–3	c. r. q.	
	13	15/16.iii	198	5·96	W., 4–N.W., 6	3–6	c.	
	14	12/13.iv	214	4·31	S.E., 4–S., 2	3	c. cl.	
	15	20/21.v	327	4·97	S., 3–S.W., 4	3	o.–cl.	
	16	6/7.vi	370	4·61	N.E., 4	3–4	fn. cl.	
	17	28/29.vii	382	5·06	S.S.E., 2	3	c.–o. r.	
		1938.						
M	1	21/22.i	*ca.* 105	*ca.* 5·0	W.S.W., 5	3–4	c.	c, D
	2	21.ii	*ca.* 130	*ca.* 5·0	W.N.W., 2	3	,,	c, D
	3	25.iii	*ca.* 60	*ca.* 5·0	N.W., 5–7	4	o. s.	c, D
	4	21/22.v	*ca.* 210 Q	*ca.* 6·0	S.W., 5	4	o.	c, D
	5	7/9.vii	227	5·28	E., 2–S.E., 6	2–5–1	o. p.	c, u
	6	20/21.vii	223	5·41	N.W., 2	2	,,	c, u
	7	24/25.viii	268	5·89	S.S.E., 5	4	c.	
	8	6.ix	*ca.* 30 Q	*ca.* 6·0	N., 2	1	,,	D
	9	21/22.ix	222	5·61	S.S.E., 4	3	,,	
	10	4/6.x	252	5·93	S.S.E., 5–W.S.W., 8	5	o. p.	
	11	21/23.x	254	5·36	S., 7	5	o.	
	12	8/9.xi	246	5·47	N.N.W., 4	3	,,	
	13	21/22.xi	245	5·29	W., 2	3	,,	
	14	7/9.xii	321	6·25	S.S.E., 6	5	o. r. q.	
	15	29/30.xii	248	5·08	W. 6	4	,,	
		1939.						
	16	9/11.i	253	6·17	W.N.W., 8	5	c. r. s. q.	
	17	23/24.i	242	5·56	N., 8	5	o.	
	18	11/13.ii	220	5·71	W., 7	5–6	o. p. q.	
	19	23/25.iii	237	5·60	S.E., 6	5	o.	
	20	8/9.iv	224	5·30	var., 2	3	c.	
	21	22/24.iv	251	5·52	S.S.E., 6	4	o.	
	22	7/8.v	243	4·95	S.S.E., 2	1	c.	
	23	21/22.v	227	5·34	S.E., 2	3	,,	
	24	6/8.vi	253	5·38	S.W., 5	5	,,	
	25	21/23.vi	251	5·65	N.N.E., 6	5	o.	
	26	8/10.vii	256	5·40	N.N.W., 7	5	o. p. q.	
	27	22/23.vii	235	5·41	N.N.W., 2	2	,,	
	28	4/6.viii	239	5·30	N., 2	1	b.	
	29	17/18.viii	240	5·12	?	?	?	
		1938.						
R	79	19/20.i	*ca.* 95 Q	*ca* 5·0	W.–S.W.	4–3	fn. cl.–o.	D
	80	2/3.ii	133	5·00	W.–N.W., 5	4–3	cl. r. q.	
	81	5/6.iii	*ca.* 89	*ca.* 5·0	var.	0	fn.	D

Route and number of record.	Date.	Mileage recorded.	Miles per section.	Wind.	Sea.	Weather.	Remarks (see p. 13).
	1938.						
R 82	13/14.iv	130	4·52	N.–N.E.	3–4	fn. o.	d
83	4/5.v	130 Q	4·69	N.E.–E.	4–3	fn. cl.	d
84	18/19.v	128	4·49	N.	3–4	o. r. q.	
85	15/16.vi	131	4·21	N.W., 4	3	fn. c. cl.	
86	13/14.vii	129	4·20	S.W., 4	3	c. cl. p.	
87	3/4.viii	129	5·71	E.–N.E.	3–4	fn. cl.	
89	21/22.ix	133	4·89	S.–S.S.W., 4	2	,,	
90	12/13.x	120	4·90	S.W., 6–7	4	o. c. p.	
91	26/27.x	89	4·61	W., 4	2–3	fn. cl.	
93	21/22.xii	130	4·78	N. 5	4	o. s.	
	1939.						
94	22/23.iii	70+56 Q	5·60	N.W.	3–4	cl. r. q.	d
95	29/30.iii	126	4·85	E., 4	3	fn. z.	
96	26/27.iv	133	5·12	N.E., 4–5	3	—	
97	20/21.v	134	5·58	N., 2	1	z.	
98	8.vi	121	6·37	N.E., 3	2	—	
99	5/6.vii	126	5·16	S.W., 5–6	4	o. cl.	
100	9/10.viii	*ca.* 40+40 Q	*ca.* 5·0	S.W., 6	4	—	d
101	16/17.viii	133	5·22	var., 2	1	fn. cl.	
	1938.						
S 1	4/6.ii	348	5·01	S., 5–4	4	cl.	
2	12/iii	*ca.* 30	*ca.* 5·0	S.W., 1	2	f.	D
4	28/29.v	352	5·44	E., 3–4	2–3	o. r.	
5	25/26.vi	312	4·98	S.W., 3–N.W., 6	2–4	—	
6	22/24.vii	353	5·09	E., 2–N.N.W., 3	1–2	c.	
7	20/21.viii	396	5·83	W., 6–7	5	c. cl.	
	1939.						
V 1	2.iv	*ca.* 130	*ca.* 5·5	S.E., 4–5–4	5–4	—	D
2	20/21.iv	243	5·33	W.N.W., 6	6	fair	
3	20/22.v	302	4·72	var., 2	2	fn.	
4	8/9.vii	288	4·94	N.E., 5–6	5	—	
5	22/23.vii	306	5·40	N.W., 2–N.E., 4	4	—	
6	*ca.* 19.viii*	*ca.* 295*	*ca.* 5·0*	?	?	?	*
	1938.						
Z 1	19/21.ii	455	5·91	N.W., 3–N.N.E., 5–W., 3	1–4–2	—	c
2	12/14.iii	178	5·35	S.W., 3–S.S.W., 4	2–3	—	c.
3	24/26.iii	431	5·27	S.W., 5–var. 2–W., 3–N.W., 4	3–4	—	c, u
4	14/15.iv	445	4·85	N.W., 3–N., 4	2–3	—	,,
7	17/18.vii	400	4·97	N.W.	2	c. o.	,,
8	7/8.viii	399	5·70	E.	0–2	c. cl.	
9	4/5.ix	373	4·72	N.–N.E.	2–0	fn. cl.	
10	16/17.x	333	5·60	S.W., 5–6	3–4	c. cl. o.	
11	13/14.xi	286	5·70	S.W., 5–6	4	r.–cl.–c.	
12	25/26.xii	293	5·92	S.W., 3–4	3	o.–cl.–c.	
	1939.						
13	5/6.ii	311	5·66	S.W., 5–4	3	o.	
14	5/6.iii	321	5·99	S., 5–S.W.–W., 6	4	c. cl.	
15	15/16.iv	319	5·28	S.W., 5–6	4–6	cl. o.	
16	14/15.v	159+132 Q	5·29	E.–S.E., 2	2	o.	d
17	11/12.vi	309	5·30	N.E.–N., 5	4–3–6	c. cl. p.	
18	11/12.vii	*ca.* 296	*ca.* 4·6	N.W.–S.W., 5	4–3	o.	V
19	13/14.viii	315	5·00	N., 2–4	2	fn.	

* No exact data : log form not returned on account of outbreak of war.

EXPLANATION OF PLATES I TO V.

Monthly charts have been prepared to show the position, extent, direction, dates and times of the beginning and end, and the periods of daylight and darkness for each record taken during 1938 and 1939, except those of the V line, which are given in a subsequent paper dealing with this Faroe–Shetland Channel line. The dates of the V line records, however, are given (April, May, July and August, 1939) to show the time relation to other lines.

When two or more records were taken within a month on the same line, one of them, if very near to the beginning or the end of the month, may be placed on the chart for the preceding or following month, if that month should lack such a record.

Position, Extent and Direction.

The position and extent of each record is shown by a line against which is placed its particular reference letter and number thus : A^1, A^2, etc. If a record is considered to be only of qualitative value, due to some slight defect, it is shown as a broken line. A half arrow-head at one end of the line indicates in which direction the recorder was towed. The number against the beginning of a line indicates the position at which the recorder was put down expressed in miles distance from the lighthouse or light-vessel marking the normal beginning of the record (see Text-fig. 1 and the description of each line given in the text, particularly regarding the beginnings of the B and E lines shown as minus quantities). The number at the end of a line, against the arrow-head, indicates in the same way the position at which the recorder was hauled up, or in the case of a mechanical failure (marked D in the summary list), the approximate position at which it is estimated the mechanism stopped (calculated as shown under " mileage recorded " in the explanation to the summary list given above).

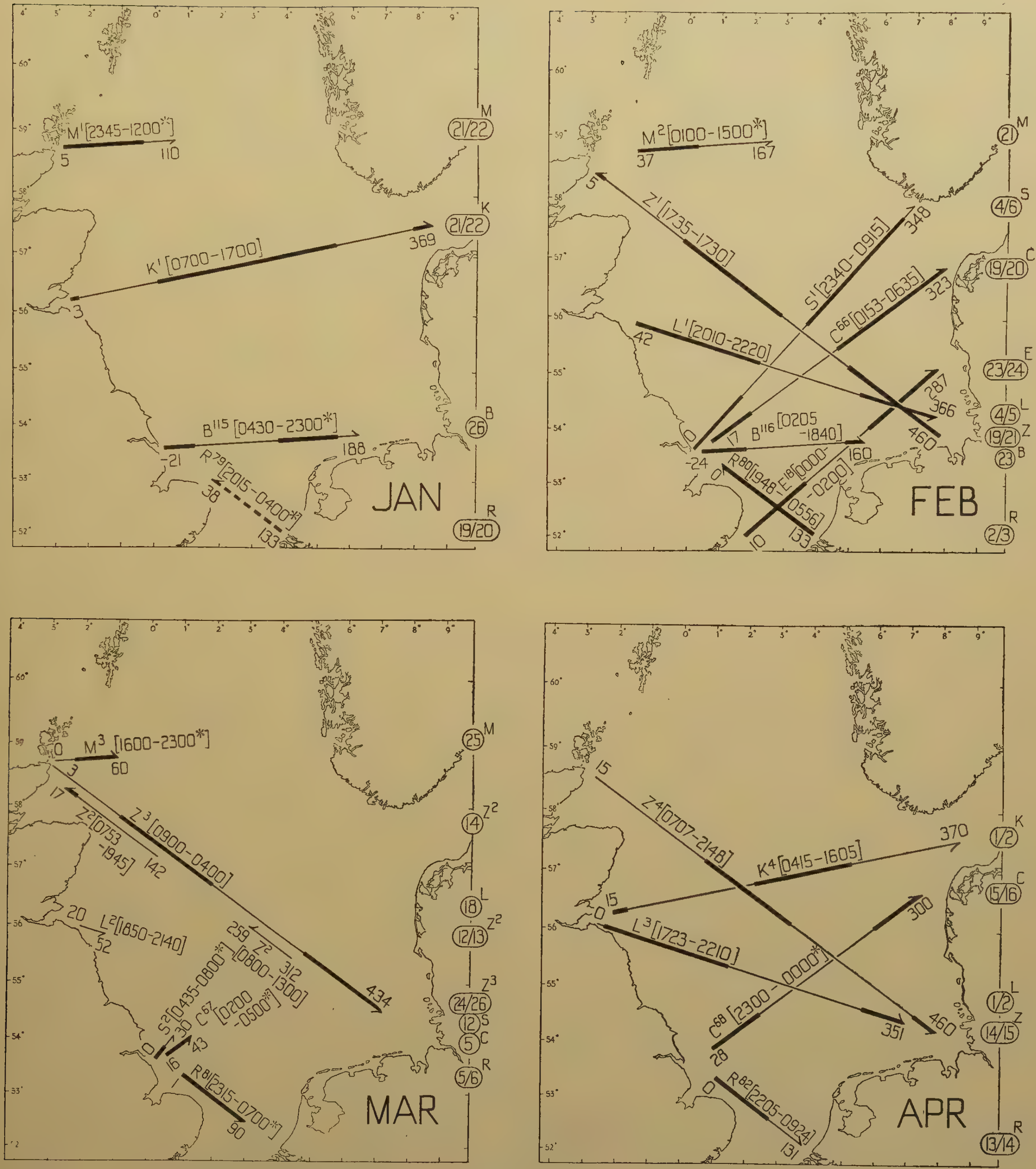
Dates and Times.

The dates appear as enclosed numbers on the right-hand margin of each chart in a position opposite, or nearly opposite, to the eastern end of the line concerned (except for dates of V line records which are shown at the top left-hand corners). Against each number, in an index position, is the letter of the line to which the date or dates refer. The times of the beginning and end of a record appear in brackets along the side of the line concerned (expressed in the 24-hour system). In the case of a mechanical failure resulting in a stoppage of the record, (marked D in the summary list) the estimated time of the end of the record is only approximate and is marked by an asterisk.

Daylight and Darkness.

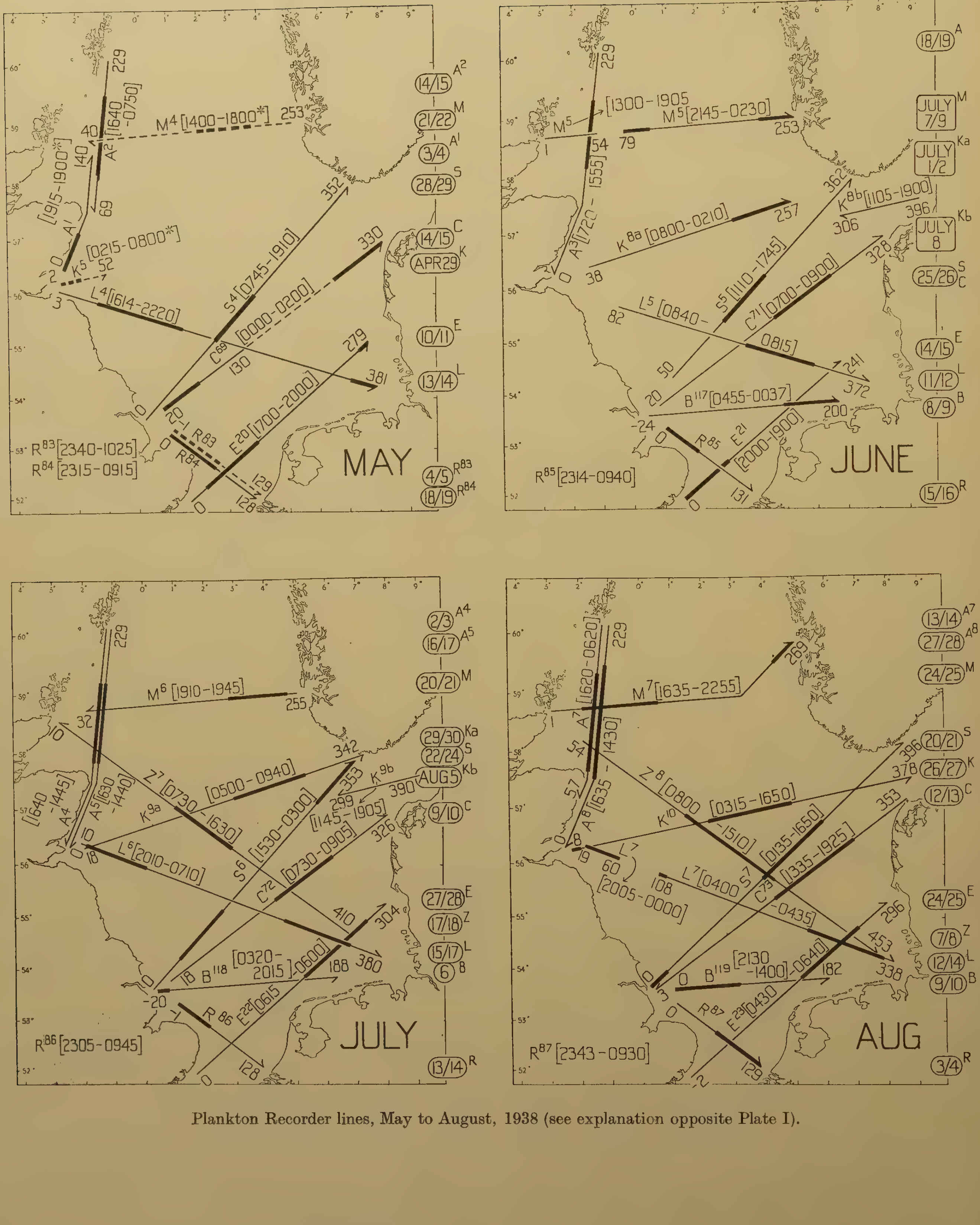
The parts of a record taken between sunset and sunrise are shown by a thicker line than the parts taken in the daytime.

PLATE I


M^{1}[2345-1200*]
5
110
21/22 M
K^{1}[0700-1700]
3
369
21/22 K
B^{115}[0430-2300*]
-21
188
26 B
R^{79}[2015-0400*]
38
133
19/20 R
JAN
M^{2}[0100-1500*]
37
167
21 M
Z^{1}[1735-1730]
5
S^{1}[2340-0915]
348
4/6 S
C^{66}[0153-0635]
323
19/20 C
L^{1}[2010-2220]
42
23/24 E
287
366
4/5 L
B^{116}[0205-1840]
0
17
-24
460
19/21 Z
23 B
160
R^{80}[1948-0556]
E^{18}[0000-0200]
0
10
133
FEB
2/3 R
M^{3}[1600-2300*]
0
3
60
25 M
17
Z^{2}[0753-1945]
Z^{3}[0900-0400]
142
14 Z^{2}
20
L^{2}[1850-2140]
52
18 L
12/13 Z^{2}
259
Z^{2}[0800-1300]
312
S^{2}[0435-0800*]
C^{67}[0200-0500*]
434
24/26 Z^{3}
12 S
0
30
43
5 C
16
R^{81}[2315-0700*]
90
5/6 R
MAR
15
Z^{4}[0707-2148]
370
1/2 K
K^{4}[0415-1605]
15
0
15/16 C
L^{3}[1723-2210]
300
C^{68}[2300-0000*]
28
351
460
1/2 L
14/15 Z
0
R^{82}[2205-0924]
131
APR
13/14 R

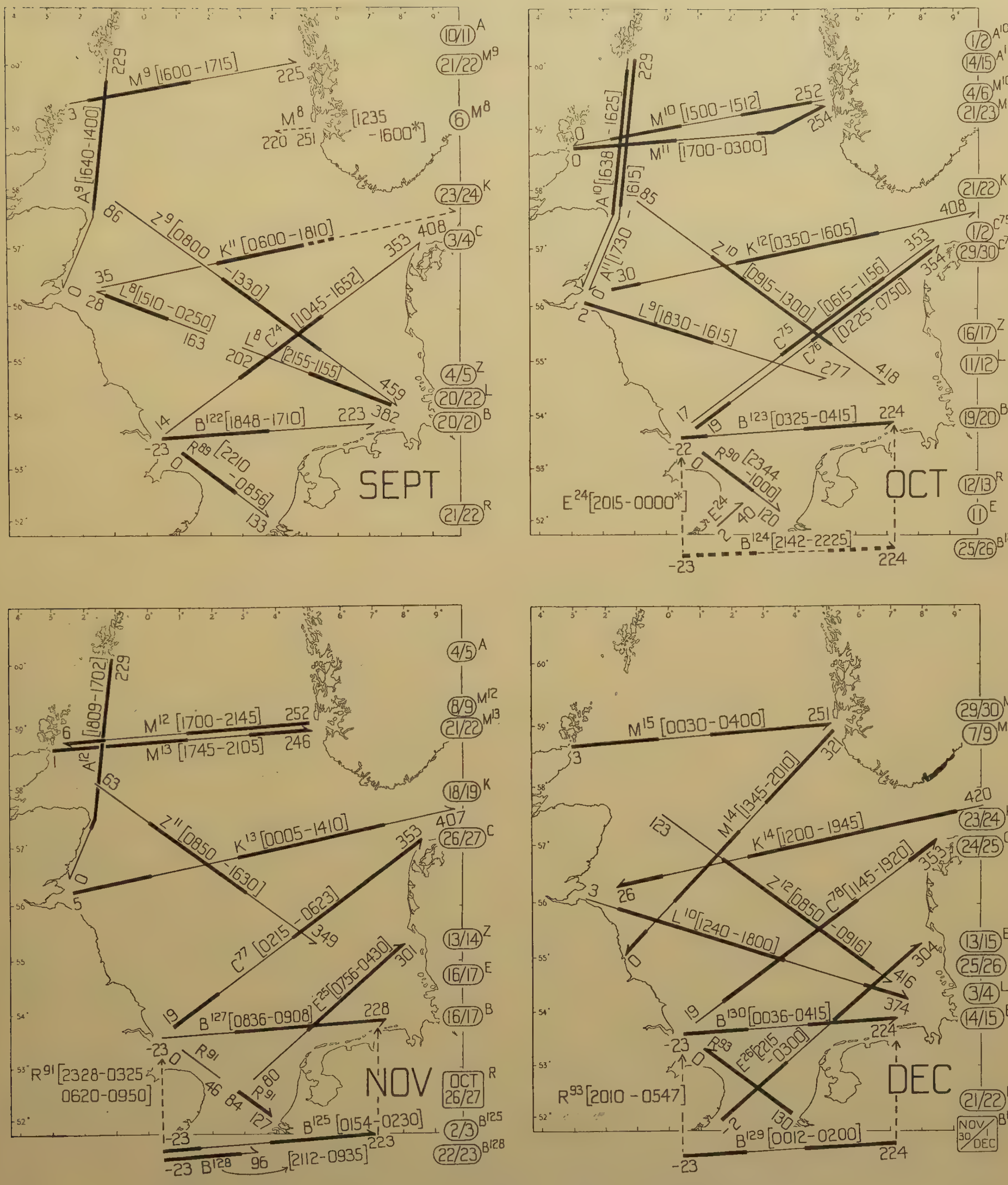
Plankton Recorder lines, January to April, 1938 (see explanation on the opposite page).

PLATE II


MAY
M⁴ [1400-1800*] 253
A² [1640-0750]
A¹ [1915-1900*]
K⁵ [0215-0800*]
L⁴ [1614-2220]
S⁴ [0745-1910]
C⁶⁹ [0000-0200]
E²⁰ [1700-2000]
R⁸³ [2340-1025]
R⁸⁴ [2315-0915]
14/15 A²
21/22 M
3/4 A¹
28/29 S
14/15 C
APR 29 K
10/11 E
13/14 L
4/5 R⁸³
18/19 R⁸⁴
JUNE
M⁵ [1300-1905]
M⁵ [2145-0230]
A³ [1720-1555]
K⁸ᵃ [0800-0210]
K⁸ᵇ [1105-1900]
S⁵ [1110-1745]
C⁷¹ [0700-0900]
L⁵ [0840-0815]
B¹¹⁷ [0455-0037]
E²¹ [2000-1900]
R⁸⁵ [2314-0940]
18/19 A
JULY 7/9 M
JULY 1/2 Ka
JULY 8 Kb
25/26 S C
14/15 E
11/12 L
8/9 B
15/16 R
JULY
M⁶ [1910-1945]
A⁴ [1640-1445]
A⁵ [1630-1440]
Z⁷ [0730-1630]
K⁹ᵃ [0500-0940]
K⁹ᵇ [1145-1905]
S⁶ [1530-0300]
C⁷² [0730-0905]
L⁶ [2010-0710]
B¹¹⁸ [0320-2015]
E²² [0615-0600]
R⁸⁶ [2305-0945]
2/3 A⁴
16/17 A⁵
20/21 M
29/30 Ka
22/24 S
AUG 5 Kb
9/10 C
27/28 E
17/18 Z
15/17 L
6 B
13/14 R
AUG
A⁷ [1620-0620]
A⁸ [1635-1430]
M⁷ [1635-2255]
Z⁸ [0800-1510]
K¹⁰ [0315-1650]
L⁷ [2005-0000]
L⁷ [0400-0435]
S⁷ [0135-1650]
C⁷³ [1335-1925]
B¹¹⁹ [2130-1400]
E²³ [0430-0640]
R⁸⁷ [2343-0930]
13/14 A⁷
27/28 A⁸
24/25 M
20/21 S
26/27 K
12/13 C
24/25 E
7/8 Z
12/14 L
9/10 B
3/4 R

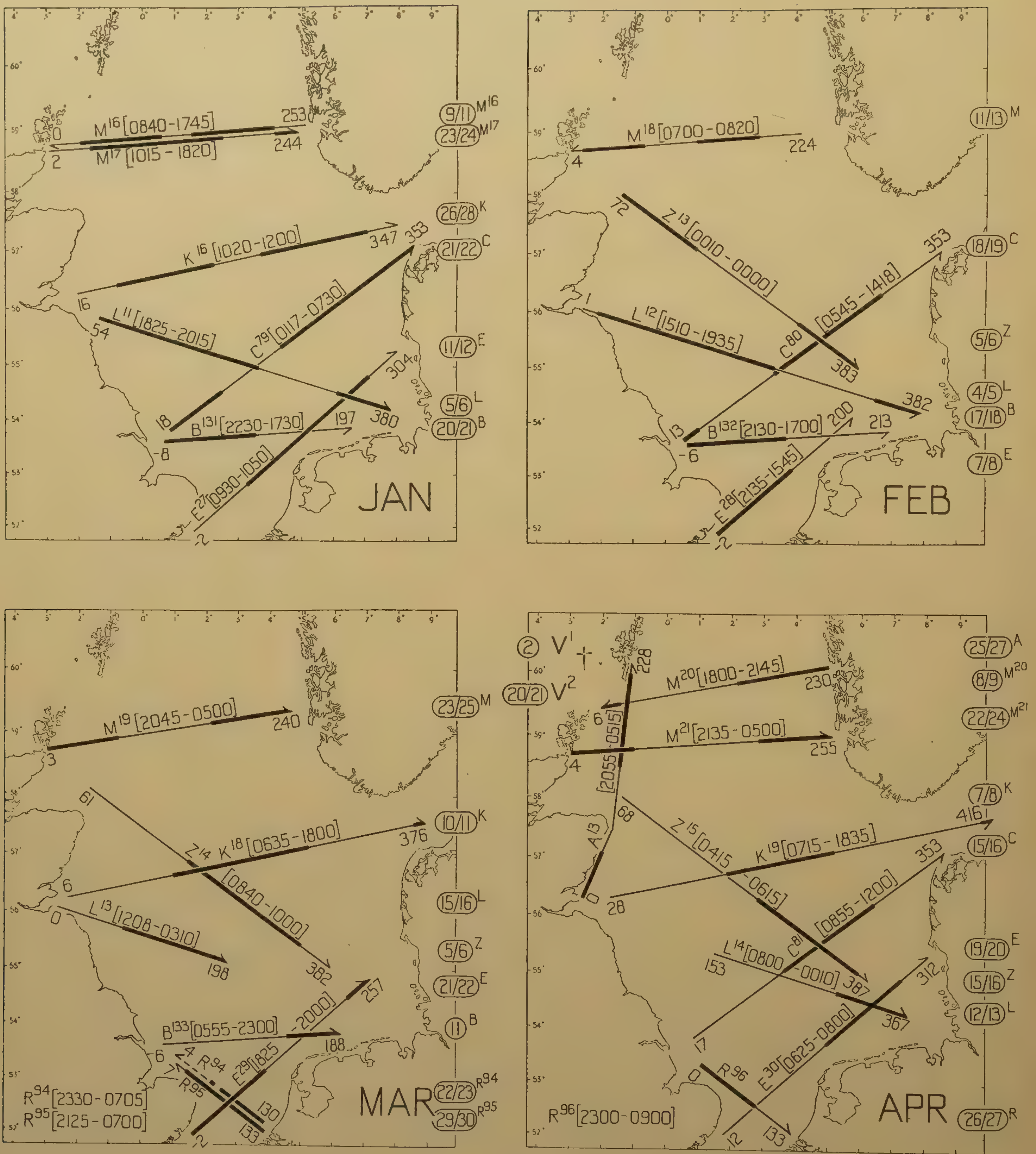
Plankton Recorder lines, May to August, 1938 (see explanation opposite Plate I).

PLATE III


SEPT
M9 [1600-1715]
229
225
3
A9 [1640-1400]
M8 [1235 -1600*]
220 251
Z9 [0800 -1330]
86
K11 [0600-1810]
35
0
28
L8 [1510-0250]
163
353
408
L8 C74 [1045-1652]
202
[2155-1155]
459
382
14
B122 [1848-1710]
223
-23
R89 [2210 -0856]
0
133
(10/11) A
(21/22) M9
(6) M8
(23/24) K
(3/4) C
(4/5) Z
(20/22) L
(20/21) B
(21/22) R
OCT
229
A10 [1638 -1625]
M10 [1500-1512]
252
254
0
M11 [1700-0300]
A11 [1730 - 1615]
85
0
30
K12 [0350-1605]
408
Z10 [0915-1300]
418
L9 [1830-1615]
2
277
C75 [0615-1156]
C76 [0225-0750]
353
354
17
19
B123 [0325-0415]
224
-22
R90 [2344 -1000]
0
120
E24 [2015-0000*]
E24
40
2
B124 [2142-2225]
-23
224
(1/2) A10
(14/15) A11
(4/6) M10
(21/23) M11
(21/22) K
(1/2) C75
(29/30) C76
(16/17) Z
(11/12) L
(19/20) B
(12/13) R
(11) E
(25/26) B124
NOV
229
A12 [1809-1702]
M12 [1700-2145]
252
6
1
M13 [1745-2105]
246
63
Z11 [0850 -1630]
K13 [0005-1410]
407
0
5
353
C77 [0215 -0623]
349
E25 [0756-0430]
301
19
B127 [0836-0908]
228
-23
0
R91
R91 [2328-0325 0620-0950]
46
84
R91
80
127
B125 [0154-0230]
-23
223
-23 B128 96 [2112-0935]
(4/5) A
(8/9) M12
(21/22) M13
(18/19) K
(26/27) C
(13/14) Z
(16/17) E
(16/17) B
OCT 26/27 R
(2/3) B125
(22/23) B128
DEC
M15 [0030-0400]
251
3
32
M14 [1345-2010]
123
0
K14 [1200-1945]
420
3
26
Z12 [0850 -0916]
C78 [1145-1920]
353
L10 [1240-1800]
416
304
374
19
B130 [0036-0415]
224
-23
R93
E26 [2215 -0300]
0
2
130
R93 [2010 - 0547]
B129 [0012-0200]
-23
224
(29/30) M15
(7/9) M14
(23/24) K
(24/25) C
(13/15) E
(25/26) Z
(3/4) L
(14/15) B
(21/22) R
NOV 30 / 1 DEC B129

Plankton Recorder lines, September to December, 1938 (see explanation opposite Plate I.).

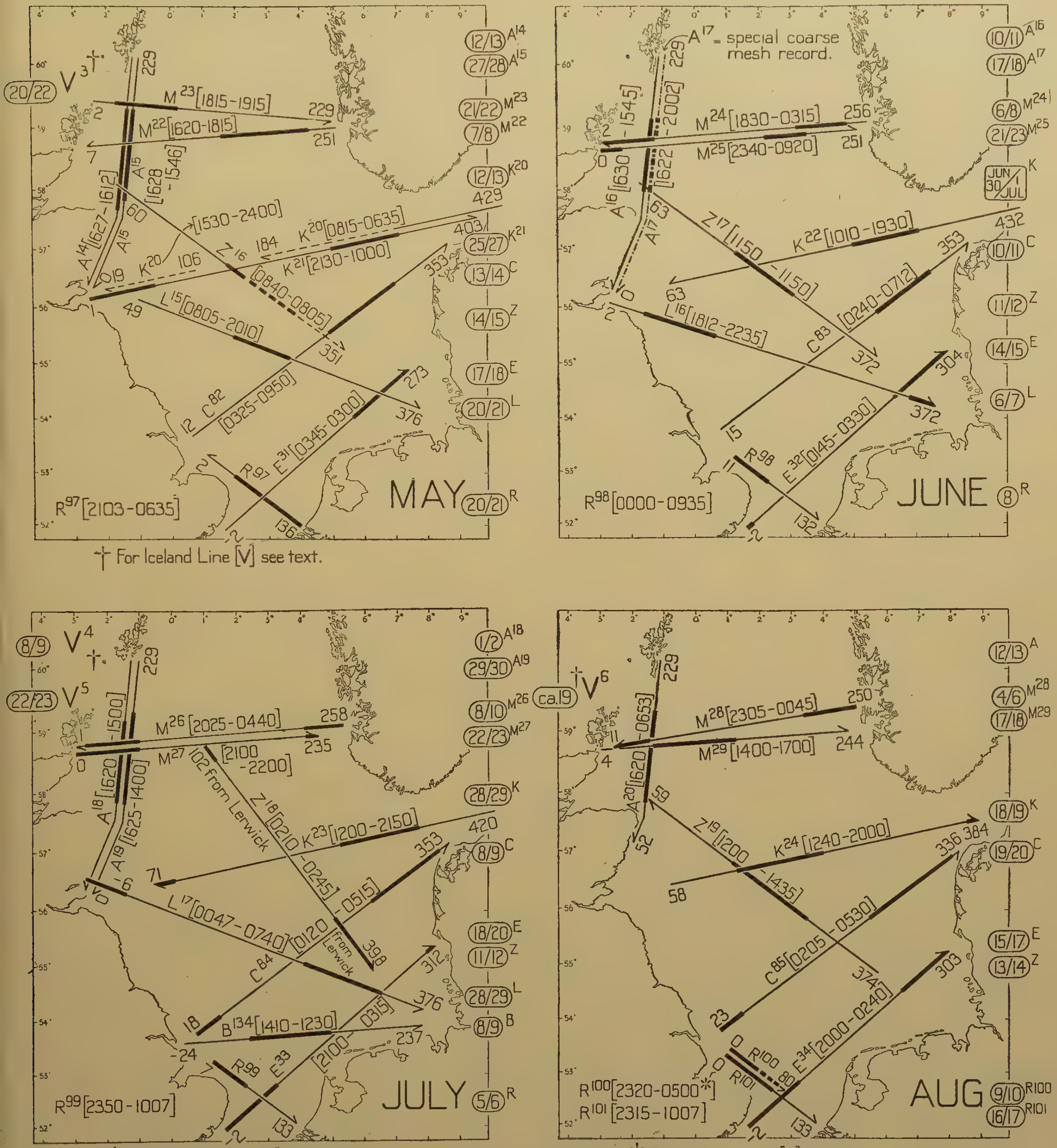
PLATE IV


JAN
M16 [0840-1745]
M17 [1015-1820]
0
2
253
244
9/11 M16
23/24 M17
26/28 K
21/22 C
11/12 E
5/6 L
20/21 B
K16 [1020-1200]
16
347
353
L11 [1825-2015]
54
380
C79 [0117-0730]
18
B131 [2230-1730]
-8
197
E27 [0930-1050]
-2
304
FEB
M18 [0700-0820]
4
224
11/13 M
Z13 [0010-0000]
72
383
18/19 C
5/6 Z
4/5 L
17/18 B
7/8 E
L12 [1510-1935]
1
382
C80 [0545-1418]
13
353
B132 [2130-1700]
-6
213
E28 [2135-1545]
-2
200
MAR
M19 [2045-0500]
3
240
23/25 M
Z14 [0840-1000]
61
382
K18 [0635-1800]
6
376
10/11 K
L13 [1208-0310]
0
198
15/16 L
5/6 Z
21/22 E
11 B
B133 [0555-2300]
6
188
E29 [1825-2000]
-2
257
R94
R95
4
1
130
133
R94 [2330-0705]
R95 [2125-0700]
22/23 R94
29/30 R95
APR
② V1
20/21 V2
228
A13 [2055-0515]
0
M20 [1800-2145]
6
230
M21 [2135-0500]
4
255
25/27 A
8/9 M20
22/24 M21
7/8 K
15/16 C
19/20 E
15/16 Z
12/13 L
26/27 R
Z15 [0415-0615]
68
387
K19 [0715-1835]
28
416
C81 [0855-1200]
17
353
L14 [0800-0010]
153
367
E30 [0625-0800]
12
312
R96
0
133
R96 [2300-0900]
4°
3°
2°
1°
0°
1°
2°
3°
4°
5°
6°
7°
8°
9°
60°
59°
58°
57°
56°
55°
54°
53°
52°

† For Iceland Line [V] see text

Plankton Recorder lines, January to April, 1939 (see explanation opposite Plate I).

PLATE V


MAY
20/22 V³ †
M²³[1815-1915]
M²²[1620-1815]
229
251
2
7
A¹⁵ [1628 -1546]
A¹⁴[1627-1612]
A¹⁵
60
19
K²⁰
106
Z¹⁶
184
[1530-2400]
K²⁰[0815-0635]
K²¹[2130-1000]
429
403
[0840-0805]
351
353
L¹⁵[0805-2010]
49
376
C⁸²[0325-0950]
12
E³¹[0345-0300]
273
R⁹⁷
136
R⁹⁷[2103-0635]
12/13 A¹⁴
27/28 A¹⁵
21/22 M²³
7/8 M²²
12/13 K²⁰
25/27 K²¹
13/14 C
14/15 Z
17/18 E
20/21 L
20/21 R
JUNE
A¹⁷ = special coarse mesh record.
229
-1545]
-2002]
M²⁴[1830-0315]
M²⁵[2340-0920]
256
251
2
0
A¹⁶[1630
[1622
A¹⁷
63
Z¹⁷[1150 -1150]
K²²[1010-1930]
432
353
[0240-0712]
C⁸³
L¹⁶[1812-2235]
63
2
0
372
372
15
304
E³²[0145-0330]
R⁹⁸
11
132
R⁹⁸[0000-0935]
10/11 A¹⁶
17/18 A¹⁷
6/8 M²⁴
21/23 M²⁵
JUN 30 / 1 JUL K
10/11 C
11/12 Z
14/15 E
6/7 L
8 R
JULY
8/9 V⁴ †
22/23 V⁵
229
-1500]
M²⁶[2025-0440]
258
235
1
0
M²⁷
[2100 -2200]
102 from Lerwick
A¹⁸[1620
A¹⁹[1625-1400]
Z¹⁸[0210-0245]
K²³[1200-2150]
420
353
71
-0515]
-6
0
L¹⁷[0047-0740]
[0120
[from Lerwick
398
C⁸⁴
312
376
18
B¹³⁴[1410-1230]
-0315]
237
-24
[2100-
E³³
R⁹⁹
133
R⁹⁹[2350-1007]
1/2 A¹⁸
29/30 A¹⁹
8/10 M²⁶
22/23 M²⁷
28/29 K
8/9 C
18/20 E
11/12 Z
28/29 L
8/9 B
5/6 R
AUG
ca.19 † V⁶
229
-0653]
M²⁸[2305-0045]
M²⁹[1400-1700]
250
244
11
4
A²⁰[1620
59
52
Z¹⁹[1200 -1435]
K²⁴[1240-2000]
384
336
58
C⁸⁵[0205-0530]
374
23
303
E³⁴[2000-0240]
R¹⁰⁰
R¹⁰¹
0
0
80
133
R¹⁰⁰[2320-0500*]
R¹⁰¹[2315-1007]
12/13 A
4/6 M²⁸
17/18 M²⁹
18/19 K
19/20 C
15/17 E
13/14 Z
9/10 R¹⁰⁰
16/17 R¹⁰¹

† For Iceland Line [V] see text.

† For Iceland Line [V] see text

† For Iceland Line [V] see text

Plankton Recorder lines, May to August, 1939 (see explanation opposite Plate I).

[*Hull Bulletins of Marine Ecology, No. 8, Vol. II, pp. 19–46, Plates VI–XXXVIII, Sept., 1941.*]

CONTINUOUS PLANKTON RECORDS:

PHYTOPLANKTON IN THE NORTH SEA, 1938–39

PART I.—DIATOMS

BY

C. E. LUCAS, B.Sc.

(Assisted by W. MACNAE, B.Sc.)

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Introduction : Material and Methods.

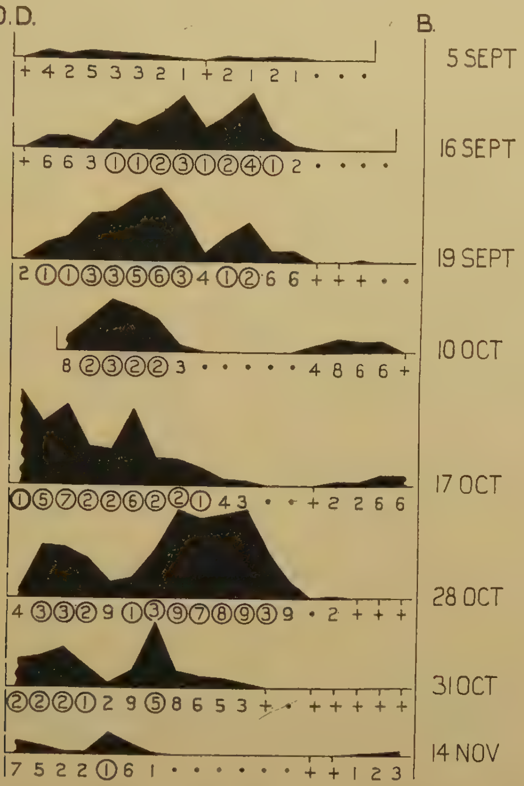
The Plankton Recorder survey was extended at the beginning of 1938 to cover the northern as well as the southern North Sea. In addition to those forming the 1932–37 survey (see Lucas, 1940, ' Bulletin ' No. 3) an extra line ran from Hull towards Oslo, three ran from Leith to Hamburg, Copenhagen and Lerwick, and two from the Pentland Firth to Hamburg and Norway. That from Hull towards Oslo was discontinued at the end of 1938 so that the gear could be used in 1939 on an experimental line across the opening to the Faroe–Shetland Channel, described in a later ' Bulletin.' The war suspended all work at sea after August, 1939, and since it was uncertain when it could be resumed, we have thought it desirable to publish at once the data for 1938 and the part of 1939. The present paper deals only with the Diatoms. The account of the Dinoflagellates and Phaeocystis has been postponed for reasons of economy; all the data has been prepared for publication, and we hope to present it in the next 'Bulletin.' The relevant zooplankton data should appear in the two subsequent numbers.

Full details concerning the shooting and hauling of the Recorders during the two years appears in 'Bulletin' No. 7 (Plates I to V and Record List). As in the earlier series there are rather more records for the phytoplankton than for the zooplankton, mainly due to the extended autumn programme in the Southern Bight. It will be seen that occasionally (*e. g.* July, 1938) records at the beginning or end of a month have been allocated to the previous or subsequent month for convenience, usually to provide the most valuable combination of dates for illustrating the changing time picture. On the other hand, although the calendar month has not been strictly adhered to, it was clearly a convenient unit, and in no case is the record more than a few days displaced *nor* has a period of more than 31 days been used. In all some 48,000 miles of record were obtained.

As before, mechanical defects have occurred sometimes, although the new developments in the machine (Hardy, 1939, 'Bulletin' No. 1) led to an appreciable decrease after June, 1938. General principles outlined in 'Bulletins' Nos. 1, 2 and 7 are followed here, certain defective records being rejected, some discarded in part, and a few being utilized with the knowledge that a part of the plankton may have been lost (details of such defective and "qualitative" records are also in 'Bulletin' No. 7). Unfortunately it has not been possible to obtain adequate sampling in every month (March, 1938, being a particular example), but in most months a set of traverses is available which should indicate the principal features of the phytoplankton in the North Sea for that period. Since these are usually the same for each month they provide standards for comparison and reference in so far as they are suitably placed. Whilst they are grouped in periods of approximately one month, we should remember that there may be a considerable time lag between the first and the last of a set, and give this due regard when necessary (see Plates I to V of 'Bulletin' No. 7). Sometimes there is more than one record on a line during the month (*e. g.* the Leith–Lerwick route during the summer and the Hull–Bremen route in the autumn). In the series of maps these have been arranged where possible "in parallel" (the earlier record above) and bracketed. When this was not possible, the extra data have been recorded in the margin (*e. g.* Plate IX); the numerals I, II or III for the Bremen route and I or II for the Lerwick route give the order in which the records were obtained.

There have been no important changes in the methods of analysis since the introduction in 1937 of the system for providing estimates of organisms per mile in blocks of ten miles ('Bulletin' No. 3, Vol. I, p. 75). The lengths of silk equivalent to the ten-mile blocks are calculated for each roll and representative portions of each examined for phytoplankton: the pieces are then cut off and passed to the zooplankton workers. Thereafter they are stored for any future use: where Phaeocystis is present in quantity, one-half is scraped for an estimate of the volume before being stored.

There has necessarily been a change in the method of presentation. For reasons of economy we can no longer consider results from each route separately, as in ‘ Bulletin ’ No. 3 ; the records have been arranged on maps, and in this form will provide the main basis for reference. With the complex network of lines it was impossible any longer to continue with the simple graphical methods of the earlier ‘ Bulletins ’ ; in its place we have adopted a system of symbols to represent the numbers per mile found on each block. *Rhizosolenia styliformis* and *Biddulphia sinensis* are shown on large maps at six to the page (*e. g.* Plate VIII) ; sets of symbols show the general distribution, whilst the numerical values denote the varying quantities with more precision. The two methods may be compared by reference to Text-fig. 1, in which several records of *R. styliformis* on the Bremen Line have been reproduced for the period September–November, 1937, in both methods. For scales see Text-fig. 4 in ‘ Bulletin ’ No. 3, and Plate IX here. (Note that for convenience the graphs in the former were limited in height.)



Text-fig. 1.—Graphs and symbols showing the abundance of *Rhizosolenia styliformis* between the Outer Dowsing (O.D.) and the Borkum (B.) light-vessels in the autumn of 1937 according to the earlier (graphical) and the present (symbolical) systems. For scales see ‘ Bulletin ’ No. 3, Vol. I, Text-fig. 4, and Plate IX in the present paper.

Symbols only have been used for the other diatoms and the different diagrams consist of the following types :

(1) All the data are shown on monthly maps at twelve to the page, so that the two years are seen facing one another (*e.g.* Plates XVI and XVII). For comparison between these symbols and those used in ' Bulletin ' No. 3, see p. 40.

(2) Twelve or six selected months have been taken to illustrate the principal features of the development (*e. g.* Plates XXXIV and XXXV). Any essential remarks about the other data are given in the text, but otherwise they are arranged as in (1).

(3) Some species which have been scarcer, or which at present seem to have less significance, have been illustrated in periods usually longer than one month (*e. g.* Plate XXXVII). The overall distribution is shown for each of these, together with the Roman numerals for the months in which the principal patches appeared. Additional remarks may be in the text.

(4) Only the overall distribution on the normal lines is shown for each year, or the years combined (*e. g.* Plate XV). It should be remembered that 1939 was incompletely sampled, so that for species which are normally abundant in the autumn it is impossible to show satisfactory comparisons over the two years. (It is important to emphasize this in relation to the whole survey, since even the omission of the data from one or two records may seriously affect the resulting picture.) For the two diatoms *Rhizosolenia calcar-avis* and Dactyliosolen, so few traces were found that they could conveniently be referred to the months.

Clearly, when working on the ten-mile block system, one will meet with sections at the beginning or the end of the record which are of less than ten miles. For the phytoplankton we have normally used such as are over five miles as representative of that block, and have rejected the others.

Throughout the programme we have attempted to obtain more precise data than was possible in the earlier work ; there remain certain groups for which it has still been impracticable to find the time required for detailed analysis, and these will be shown as groups (*e. g.* the group Hyalochaeta excluding *Chaetoceros decipiens* and the " Naviculoid " diatoms). There are necessarily a number of features rendering the approximations involved in this work greater than those normally made (mainly due to the difficulties of analysis within dense concentrations of mixed diatoms). On the other hand, the broad scale methods of presentation of the data and the continuous method of survey reduce the significance of such deficiencies. We are at present concerned more with the large differences which can be (and are) found within relatively short distances : these greatly exceed such errors as we have reason to expect exist in the individual data.[1] One other point concerns the depth at which the samples were obtained. For many organisms it is clear that sampling at ten metres may be even less reliable in the deeper northern waters than in the Southern Bight. Although we have been unable to investigate this further, we have reason to believe that since the phytoplankton flourishes only at relatively shallow depths, the differences will be less serious here (*cf.* Gran, 1915 ; Marshall and Orr, 1930). The general problem of relation between depth and the significance of the sample was discussed in ' Bulletin ' No. 3, and we consider that many of the conclusions made there will apply also to the deeper waters of the northern North Sea.

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[1] It is important to remember that the silk used in this work, 60 meshes to the inch, is much coarser than that normally used for collecting phytoplankton. Consequently the quantities of many of the diatoms are much smaller than those usually obtained with such nets, although we believe the differences in the quantities found *within* this method to be significant of real differences in the conditions of the sea (*cf.* discussion in ' Bulletin ' No. 3, Vol. I, p. 77).

The northern material has been analysed by C. E. L., and that for the south by W.M. Owing to Mr. Macnae's resignation from the Department to take up other work, he has been unable to assist in working up the results.

THE DISTRIBUTION OF THE DIATOMS.

As far as possible the maps have been left to speak for themselves, whilst the usual descriptive section of the text will be limited to a few additional remarks concerning material which has had to be omitted (see above) and certain points to which attention should be drawn. In addition to the series of plates reference should also be made to Text-figs. 2–5, in which the data for most of the diatoms on the southern lines has been presented in an appropriate form for comparison with ' Bulletin ' No. 3. A few results will then be reviewed briefly in the discussion at the end of the paper, when some comparisons will be made between the data for the two years, and between these and the earlier years for the southern routes. We hope that it will be possible to deal more fully in later Bulletins with some matters which have had to be omitted here or mentioned only very briefly.

As before, reference has normally been made to Lebour (1930) for identification and the names used there have been adopted. When in the text reference is made to " traces " or " patches " the former term indicates those small numbers of any diatom which are denoted by the symbol " + " on the series of maps ; the term " patches " is used for the larger concentrations denoted by the various other symbols on the scales provided.

Paralia sulcata (Ehr.). (Plate VI shows the main concentrations.)

This is not a truly planktonic diatom, but is liable to be carried into the upper layers at times of extensive disturbance. Although seldom numerous in comparison with some other diatoms, its variations should be useful in connection with water movements. Plate VI shows the marked seasonal variations together with the great decrease in 1939, particularly in the Southern Bight. We may note its general scarcity in the north-central North Sea, except in the winter months, this being in agreement with the findings of Ostenfeld (1913). The various species of Gyrosigma, shown alongside, have often a similar distribution, and were also much scarcer in 1939. In these records both were very scarce round the west coast of Norway.

Coscinodiscus spp. (Plate XXXVIII shows the main features in selected maps.)

It was impracticable to separate the species of this genus, but the large ones (mainly *C. concinnus*) have been separated from the smaller ones, which have been much scarcer on the whole ; the larger ones only are shown in the Plate, whilst in Text-fig. 4 the whole data has been used for comparison with the 1932–37 results. In addition to those shown, a few traces were found on the Leith–Copenhagen line in May, 1939. The diffuse, and more northern, distribution of 1939 should be noted. The only patches found were in the winter rather than the spring quarter. It remains possible that some of the diatoms identified here as *Thalassiosira decipiens* were in fact small Coscinodiscus, in view of well-known difficulties of identification.

Thalassiosira spp. (Including Coscinosira spp.) (Plates XXII and XXIII.)

When these were dense we did not feel that the time would justify the labour of separating Coscinosira from the main group (or the different species of Thalassiosira). *Th. decipiens* has been a common form in the earlier stages of the spring growth[1] and thereafter *Th. gravida* and *Th. Nordenskiöldii* have been the commonest species. The arrangement of patches in the north in relation to the possible entry of external waters should be noted, and also the apparent mixing of such patches in the spring of 1939. In general the group was more abundant in 1939. The persistence of patches off the north-east coast of Scotland (even up to October in 1938) is of interest in view of Ostenfeld recording (for both *Th. gravida* and *Th. Nordenskiöldii*) their large numbers off the coast of Scotland in August when they were scarce elsewhere.

Lauderia borealis Gran. (Plate XXXVIII shows the main features in selected maps.)

In addition to those shown, one or two traces appeared in December, 1938, and January, 1939. Note the much earlier north-western growth of 1939. The general contrast between the autumn-winter distribution of the southern North Sea and the spring-summer one in the north agrees well with Ostenfeld's findings, although the August–September patches off Heligoland in 1938 are apparently an exception.

Skeletonema costatum (Greville). (Plate XXXI shows the main features in selected maps.)

Other traces were found in May, November and December, 1938. It has been very spasmodic in the records and is clearly more easily lost than most diatoms

---

[1] *Cf.*, however, the note on Coscinodiscus spp. Whilst these appeared to us to be *Th. decipiens*, it remains possible that some of the isolated cells were, in fact, small Consinodiscus of the types forming the " Disco " plankton of earlier writers.

(note the modified scale). Once again autumn patches were scarce ; the recording of patches near the Skagerrak in October, 1938, is so far the only instance in these records strictly in accordance with Ostenfeld's observation of a secondary maximum.

Stephanopyxis turris (Greville). (Plate XXIX shows the overall distribution.)

It was absent from June to August inclusive in 1938, whilst the sole traces in 1939 were in April ; thus it was much scarcer in the spring of that year. Its scarcity in the northern waters is interesting in view of Ostenfeld's suggestion that it may enter " the North Sea *via* the North of Scotland " (1913, p. 419).

Dactyliosolen spp. (Plate XI shows all the records.)

A few cells were first seen on the Bergen line early in October, 1938, followed a fortnight later by a few more a little to the east. Another trace was also found off the Skagerrak in November. It is probable that the species was *D. mediterraneus*. Ostenfeld notes (1913, p. 508) that it " is carried by the current through the Faroe–Shetland Channel into the North Sea."

Leptocylindrus danicus Cleve. (Plate XXXVII shows all the records.)

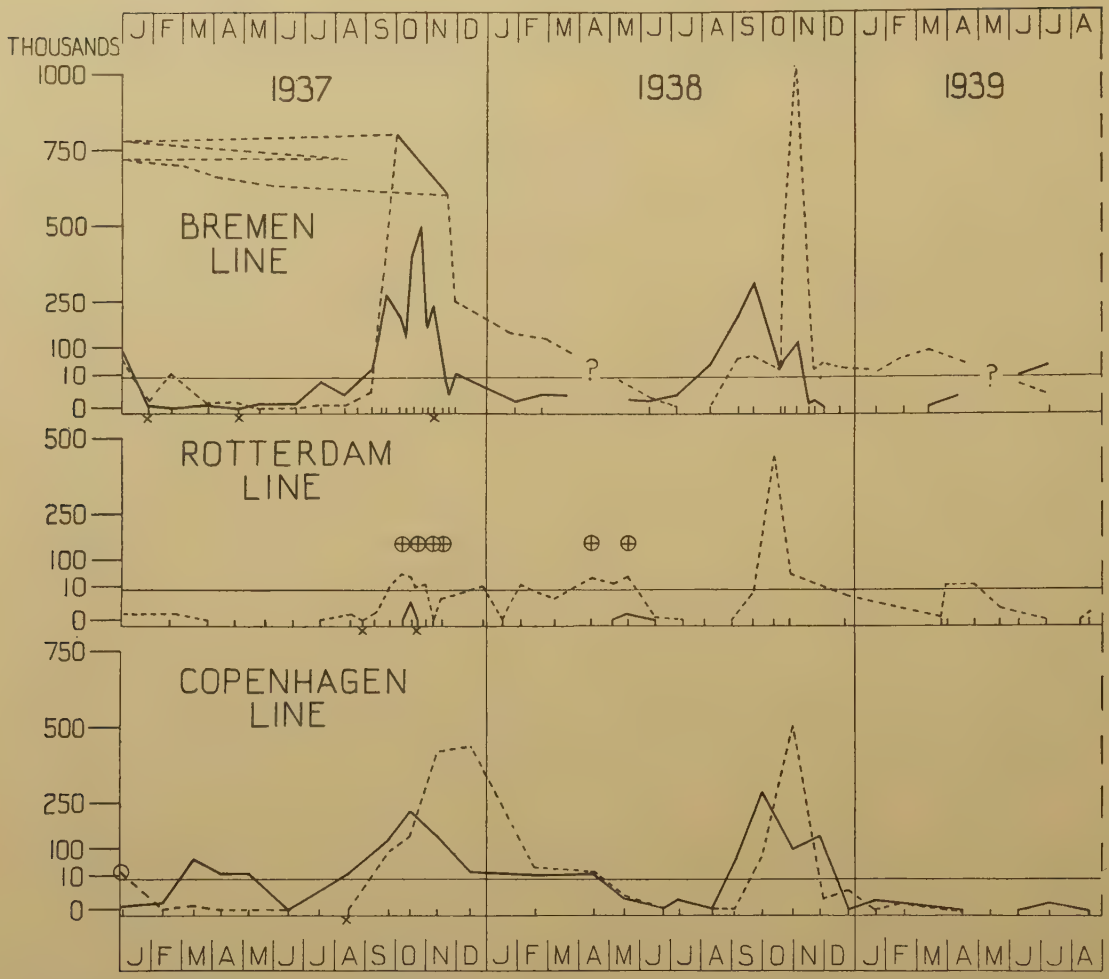
Note its generally more northern distribution in 1939. Like Skeletonema it has been very patchy in these records, probably owing to its small size.

Guinardia flaccida Castr. (Plate XXIX shows the overall distribution for each year.)

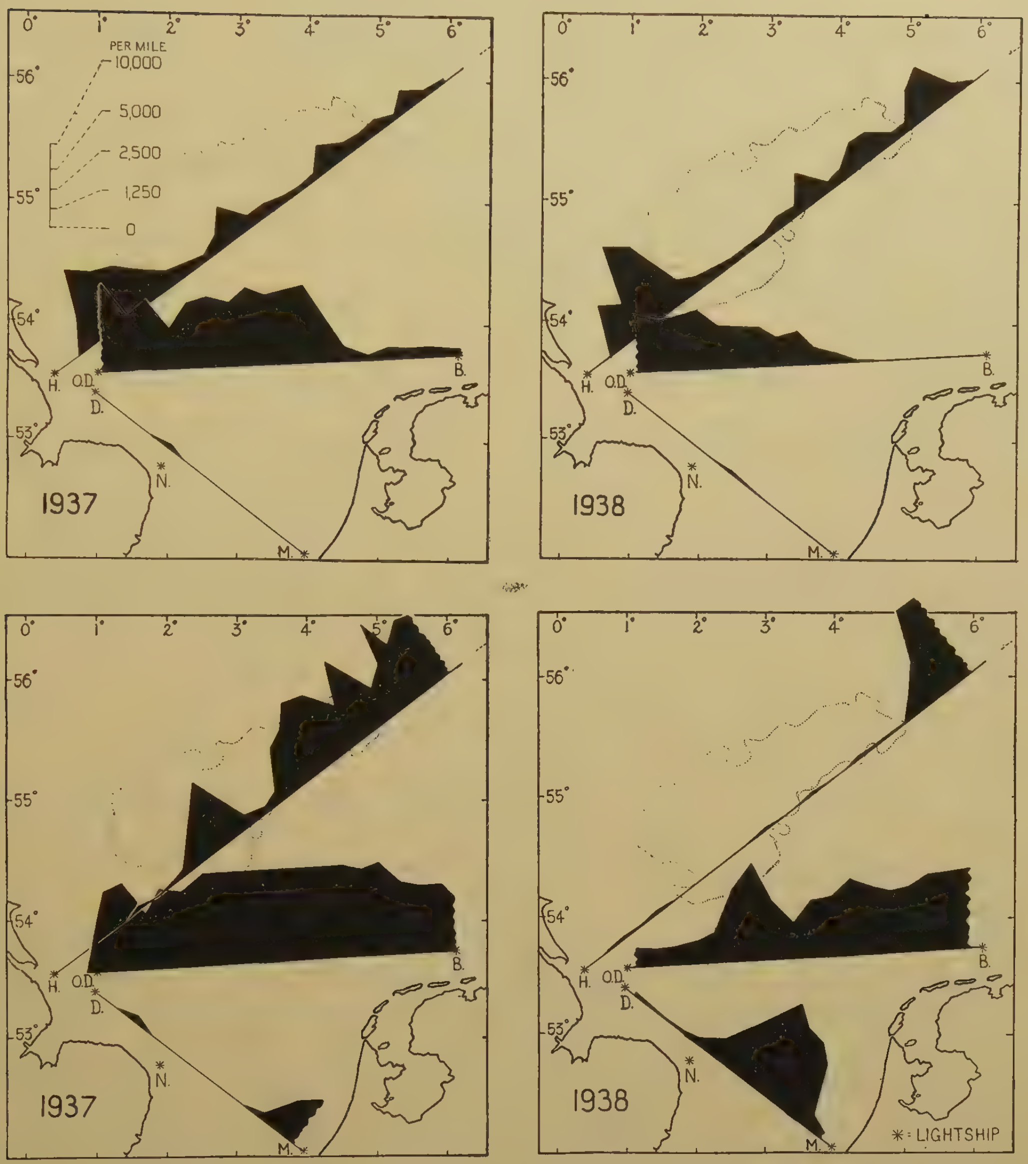
One small patch occurred near the junction of the Esbjerg and the Leith–Hamburg lines in July, 1938 ; only traces were found on other occasions. The north-western traces of 1939 appeared in July and August. We have already remarked (' Bulletin ' No. 3) that a tendency to live in deeper waters more than other forms may account for its unusual scarcity in our records.

Corethron criophilum Castr. (Plate XV shows the overall distribution for each year.)

The largest numbers were found on the Lerwick line in August, 1939, but it was not a dense patch. Previously, fair numbers had been found at the eastern end of the Faeroe line (July, 1939). In view of Ostenfeld's remarks, the few occurrences off the Skagerrak in 1938 (occurring in October) are interesting. He says " it may undoubtedly be considered an indicator of Atlantic water." Similarly the few occurrences on the Hull–Bremen and Hull–Rotterdam lines in 1932 and 1933 may prove to be important.



Text-fig. 2.—Graphs showing the fluctuations in the total numbers of *Rhizosolenia styliformis* (continuous line) and *Biddulphia sinensis* (broken line) recorded between January, 1937, and August, 1939, for comparison with Text-fig. 5 of 'Bulletin' No. 3 (1932–37). The records for the Bremen line (between Outer Dowsing and Borkum light-vessels), the Rotterdam line (between E. Dudgeon and Maas light-vessels) and the Copenhagen line (from Humber light-vessel for 250 miles towards the Hanstholm) are shown separately. Above and below are time scales in months: J., F., M., A., etc. Each point on a graph represents the total number of cells of the particular diatom found on one record; the exact position of each record in relation to the time scale is shown as a small vertical line against the base-line of the graphs. The scale of numbers is in thousands of cells per record; it should be noted that the vertical scale has been exaggerated below the 10,000 point in order to magnify the small, but often significant changes which occur when these diatoms are scarcer. The true base line, however, is also shown (*i. e.* just below point "10" on the scale). Records covering less than half the standard distance (see above) have been omitted except where indicated by an open circle; records covering less than 80 per cent. are indicated by an ×. The few traces of *R. styliformis* on the Rotterdam line are indicated by a + sign within a circle. (The high peaks of the *Biddulphia* graph for 1937 are folded over to the left for space economy.)



TEXT-FIG. 3.—Charts showing the maximal quantities of *Rhizosolenia styliformis* (above) and *Biddulphia sinensis* (below) in numbers per mile (scale inset) recorded in the years 1937 and 1938 at different points along the three lines from Hull to Bremen, Rotterdam and Copenhagen. These should be compared with similar charts for 1932–37 in Text-fig. 6 of ‘ Bulletin ’ No. 3. Note that, as in those charts, the graphs are limited in height for convenience, and some patches, *e. g.* that on the Copenhagen line in 1938, were denser than is apparent.

Bacteriastrum spp. (Plate XXV shows the main features in selected maps.)

All the records were along the Dutch-German-Danish coasts, and so it is probable that they were restricted to *B. hyalinum* Lauder as in previous years.

In addition to those shown a trace appeared near Borkum in June and November, 1938, and a small patch off the Skagerrak in August, 1939.

Rhizosolenia alata Brightw. (Plates XVI and XVII.)

The great difference between the growths of the two years should be noted. Not until June did a significant flowering appear in 1939, and even by August no cells had been seen south of the latitude of the Forth estuary. Even off the Skagerrak and in the north-west the numbers were lower in 1939. The forma *gracillima* has been undoubtedly the most abundant in these as in earlier records, but the typical form may also be common. Although the forma *indica* was seen in 1938, it was not as numerous as in 1937.

Rhizosolenia faeröense Ostenf. and *R. fragillima* Bergon. (Plate XXIII shows the important patches of July and August, 1939.)

A number of traces and one or two small patches were found at other times (mainly in the south). It seems probable that the southern ones were largely *R. fragillima*, whilst *R. faeröense* was dominant in the north-west, although identification is well known to be uncertain. In contrast to the patches shown for 1939 only one north-western trace was found in 1938 (in June).

Rhizosolenia Stolterfothii H. Pérag. (Plate XXXIV shows the main features in selected maps.)

In addition to those shown a few traces were found in April and May, 1938, and May and August, 1939. The limitation of the main patches to the Forth and the Tay estuaries and the Heligoland and Southern Bights, is a point of interest.

Rhizosolenia Shrubsolei Cleve. (Plates XVIII and XIX.)

Although this species was generally scarcer in 1939 than in 1938 (with the possible exception of May) there were significant resemblances between the two years, *e. g.* the small north-western patches in May, the larger ones off the Forth in July, and the much larger south-eastern ones from May onwards.

Rhizosolenia setigera Brightw.

A few traces, mainly along the Hull–Copenhagen line, were recorded in September and October, 1938.

Rhizosolenia styliformis Brightw. (Plates VII to XI.)

Undoubtedly this species is given undue prominence in these records as the result of its great size, but it is difficult to avoid the impression of its importance (and certainly of its significance) in understanding the North Sea cycle. The southern growths of 1938 are similar on the whole to those outlined in ‘ Bulletin ’ No. 3 for the years 1935–37, although the quantities are smaller and it was unusually scarce in October and the succeeding months. In fact, after January, 1939, no cells were found south of Lat. 55° N., and very few south of 56° N., until the small central patch appeared on the Hull–Bremen line in July. On the other hand, the recent survey gives us information about the life of *R. styliformis* outside the old area, and for the first time it is possible to follow its development over the greater part of the North Sea. What we may term the south-eastern growth in 1938 clearly extended well beyond the southern North Sea proper, but in addition we find that quite large flowerings may occur also in the waters of the north-west (particularly in the autumn). Such northern North Sea patches seem to have received little attention in the past (*cf.* Ostenfeld, 1913), and there is reason to believe that their investigation may be useful. Examination of the cell sizes (see p. 43 and Plate VII) suggests that the diatoms of the two regions may be distinguishable since those of the north-west are generally smaller than the south-eastern ones. We have further found that when, as in the autumn of 1938, the distribution of *R. styliformis* was more or less continuous over the area, it was still possible to separate the two types by this means and so to obtain some idea of the degree of mixing of the waters. The absence of the autumn data for 1939 prevents full comparison with the 1938 results, but we should compare and contrast the appreciable north-western patch of April and May. We may also note the persistent, though small, patch on the Leith–Copenhagen line which appears to carry over from the previous winter until May. Such apparently persistent centres are likely to be important, though in this case we are unable to say whether there was a similarly persistent one in 1938.

For comparison of the monthly "totals" and the "maximal" quantities with the data for 1932–37 graphs may be used which have been prepared for the three southern lines (Text-figs. 2 and 3). The general decrease in abundance in 1938 is clearly shown here. We may say that the results as a whole agree very well with the unpublished data very kindly shown to us in advance by Mr. R. S. Wimpenny, of the Ministry of Agriculture and Fisheries Laboratory, Lowestoft.

Rhizosolenia calcar-avis Schultze. (Plate XI shows all the records.)

These traces are the first recordings of this species since the survey began in 1932. Note the apparent translation in position between the findings in the two months.

Rhizosolenia hebetata semispina (Hensen). (Plates XX and XXI.)

With the exception of July, it was scarcer in the south in 1939 than in 1938. Otherwise many of the features are similar. We may note in particular the double patches on the Bergen line in the spring of both years (*cf.* several other species of diatoms) and the summer patches off the Scottish coast. The latter patches (in close association with *R. Stolterfothii*) and the very southerly patches of May, 1938, should be considered in conjunction with Ostenfeld's suggestion that this is an oceanic species which " penetrates into the North Sea by the access north of Scotland " (1913, p. 441).

Only a few cells of *R. h. hiemalis* Gran have been seen during the two years.

Chaetoceros.

Since 1935 we have separated the two subgenera Phaeoceros and Hyalochaete. The difficulties of further subdivision when diatoms are numerous (the occasions when precise identifications would be most desirable) do not justify the time required, but we have found it possible to separate *Ch. decipiens* from the Hyalochaetes, and so will present the data in three sets.

Chaetoceros s.g. Phaeoceros. (Plates XXIV and XXV.)

These have consisted largely of *Ch. borealis* and its varieties. The numbers in the two years seem to have been rather similar, 1939 being perhaps a little thinner in the south. In this group may be noted a particular tendency which is shown more or less by several forms : after a fairly widespread distribution the central region becomes empty and the patches are mainly coastal. The northern patches developed later each year than in the south.

Chaetoceros decipiens Cleve. (Plates XXVI and XXVII.)

Here again the northern patches were about a month later than in the rest of the area. On the whole it was a little scarcer in the south in 1939 than in 1938, and rather more abundant in the north. The occurrence is in general agreement with that found by Ostenfeld. In Text-fig. 4 these are included in the group for comparison with 1932–37.

Chaetoceros s.g. Hyalochaete (excluding *Ch. decipiens*). (Plates XXVIII and XXIX.)

Again the southern patches were rather weaker in 1939 and the northern ones stronger. In this group we can see that the northern patches may, as in 1939, develop even earlier than the southern ones (note, however, how heterogeneous is the group). The persistent patches off the Orkneys and Shetlands, particularly in 1939, should be noted. The group was particularly scarce on the southern lines in comparison with the dense patches found in the year 1937 (*cf.* also Text-fig. 4, in which this group and *Ch. decipiens* are combined as Total Hyalochaetes).

Biddulphia aurita (Lyngb.). (Plate XXXVI.)

In addition to those shown a few traces were also seen in March, 1938, and January, 1939. The limited coastal distribution is clearly seen (*cf.* Ostenfeld, 1913). It is unfortunate that the omission or failure of some records in April, 1938, and March, 1939, should have prevented effective comparison with the large quantities found along the Danish coast in April, 1939.

Biddulphia mobiliensis (Bail.) Grun. in Van Heurck and *B. granulata* Roper. (Plate XV shows the overall distribution for each year.)

Certain doubts regarding identity suggest that it is still advisable to combine the data for these two species. *B. mobiliensis* is definitely the more abundant of the two. No large patches were found, but in 1938 the most widespread distribution occurred in February. The few occurrences in the north-west should be compared with those for *B. regia* (with which this data is combined in Text-fig. 5 for comparison with 1932–37).

Biddulphia regia M. Schultze. (Plate XVII shows the overall distribution for each year and the large patches of 1939.)

This has been scarce at most times, and although in 1938 it was most abundant in the spring, yet only one small patch was found then (near the Maas in February). The greater numbers were in 1939 (note the occurrences in the north-west then). It is striking that for at least eight years (according to these records) it has remained relatively inconspicuous in comparison with *B. sinensis*, although it used to be regarded as an important feature of the plankton. In Text-fig. 5 this species has been combined with *B. mobiliensis* and *B. granulata* for comparison with 1932–37.

Biddulphia sinensis Grev. (Plates XII to XV.)

As with *R. styliformis* the southern distribution resembles that of the previous years fairly closely, although the numbers in the autumn of 1938 were lower than in 1937. We should note also that dense patches were never found so near to the Outer Dowsing Light as in that year, and that the occurrence on the Hull–Copenhagen line was once again limited to the water east of the Dogger Bank. On the other hand the quantities on the Rotterdam line for a brief period were the greatest found in these records: note, however, their more central position. These points are shown clearly in Text-figs. 2 and 3, where the "total" and the "maximal" distributions in time and space are given for the three southern lines.[1] The extended survey enables us to see the limited distribution in the autumn of 1938, probably a typical one (*cf.* Ostenfeld, 1908 and 1913). In view of this the appearance of small patches in the north-west in the spring of 1939 may be important; it may be compared with that for several other diatoms (*B. regia*, Ditylium and Bacillaria, etc.). Not since 1930 has the Scottish Fishery Board recorded *B. sinensis* in abundance for this region (Rep. Fish. Bd. Scot. for 1930 to 1938).

Biddulphia rhombus (Ehr.) W. Smith. (Plate XV shows the overall distribution for each year.)

Traces only were found, and their very limited occurrence in this survey amply confirms the apparent limitation which we found in the earlier work. In 1939 it seems to have been even more limited than in 1938.

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[1] Note that the patch on the Copenhagen Line in 1938 was much denser than those in 1937, although this is not apparent in Text-fig. 3, owing to the abridged scale adopted for convenience (*cf.* also Text-fig. 2).

DIATOMS	LINE	1937												1938												1939							
		J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A
PARALIA SULCATA	C	⊕	○	⊕	○	⊕	⊕	⊕	⊕	⊕	⊕	⊕	⊕	—	⊕	—	⊕	⊕	⊕	⊕	⊕	⊕	⊕	⊕	⊕	○	⊕	—	○	○	○	○	⊕
	B	⊕	⊕	⊕	⊕	⊕	⊕	⊕	⊕	⊕	⊕	⊕	—	⊕	⊕	—	—	—	⊕	⊕	⊕	⊕	⊕	⊕	⊕	⊕	⊕	⊕	—	—	—	⊕	—
	R	—	⊕	⊕	⊕	⊕	⊕	⊕	⊕	⊕	⊕	⊕	⊕	○	⊕	○	⊕	⊕	⊕	⊕	⊕	⊕	⊕	○	⊕	—	—	⊕	⊕	⊕	⊕	⊕	⊕
COSCINODISCUS SPP.	C	⊕	⊕	⊕	⊕	○	⊕	⊕	○	○	⊕	⊕	⊕	—	⊕	—	⊕	⊕	○	○	○	○	○	◑	○	○	⊕	—	⊕	○	○	○	○
	B	⊕	⊕	⊕	⊕	⊕	⊕	⊕	⊕	⊕	⊕	⊕	—	⊕	⊕	—	—	—	⊕	⊕	○	◑	⊕	⊕	○	⊕	⊕	⊕	—	—	—	○	—
	R	—	⊕	○	⊕	⊕	⊕	○	⊕	⊕	⊕	⊕	⊕	○	⊕	○	⊕	⊕	⊕	⊕	⊕	○	○	○	○	—	—	○	⊕	○	○	○	○
THALASSIOSIRA SPP. ETC.	C	○	◑	●	●	⊕	●	○	○	○	○	⊕	⊕	—	⊕	—	◑	○	○	○	○	○	◑	⊕	○	○	●	—	●	◑	●	○	○
	B	⊕	◑	●	○	●	●	○	○	⊕	◑	⊕	—	◑	⊕	—	—	—	⊕	○	○	⊕	⊕	⊕	○	○	⊕	●	—	—	—	○	—
	R	—	◑	◑	⊕	●	●	◑	○	⊕	⊕	⊕	⊕	○	○	○	⊕	⊕	○	○	⊕	○	○	⊕	○	—	—	⊕	●	⊕	○	○	○
SKELETONEMA COSTATUM	C	○	⊕	●	○	○	○	○	○	○	○	○	○	—	○	—	○	○	○	○	○	○	○	○	○	○	●	—	○	○	○	○	○
	B	⊕	⊕	●	○	○	○	○	○	○	○	○	—	○	⊕	—	—	—	○	○	○	○	○	○	○	○	⊕	⊕	—	—	—	○	—
	R	—	⊕	⊕	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	—	—	○	○	○	○	○	○
LEPTOCYLINDRUS DANICUS	C	○	○	○	⊕	○	○	○	◑	○	○	⊕	○	—	○	—	○	○	○	○	○	○	○	○	○	○	○	—	○	○	○	○	○
	B	⊕	○	⊕	○	○	○	⊕	⊕	⊕	⊕	○	—	○	○	—	—	—	●	●	○	◑	○	○	○	○	○	○	—	—	—	○	—
	R	—	○	⊕	○	○	○	○	⊕	⊕	⊕	○	○	○	○	○	○	○	●	○	◑	○	○	○	○	—	—	○	○	○	◑	○	○
GUINARDIA FLACCIDA	C	○	⊕	○	⊕	⊕	⊕	◑	⊕	○	⊕	⊕	⊕	—	⊕	—	○	○	○	○	○	⊕	○	○	○	○	○	—	○	○	○	⊕	⊕
	B	○	○	○	○	⊕	⊕	○	◑	⊕	⊕	⊕	—	○	○	—	—	—	⊕	⊕	⊕	⊕	○	○	○	○	○	○	—	—	—	○	—
	R	—	○	⊕	○	○	○	○	○	⊕	⊕	⊕	○	○	○	○	○	○	○	⊕	⊕	○	○	○	○	—	—	○	○	○	⊕	○	⊕
RHIZOSOLENIA SHRUBSOLEI	C	⊕	⊕	◑	⊕	⊕	○	◑	○	◑	⊕	⊕	⊕	—	⊕	—	⊕	○	⊕	○	⊕	◑	⊕	⊕	○	○	⊕	—	○	○	⊕	○	◑
	B	○	⊕	⊕	○	⊕	⊕	⊕	◑	⊕	⊕	○	—	⊕	⊕	—	—	—	●	●	●	●	⊕	⊕	○	○	○	○	—	—	—	◑	—
	R	—	⊕	◑	○	⊕	○	○	○	○	⊕	○	○	○	⊕	⊕	○	⊕	●	⊕	●	○	○	○	○	—	—	⊕	◑	○	○	○	●
RHIZOSOLENIA STOLTERFOTHII	C	○	⊕	⊕	○	○	○	⊕	⊕	◑	○	⊕	⊕	—	⊕	—	⊕	○	○	○	○	○	⊕	○	○	○	○	—	○	○	○	○	○
	B	○	○	⊕	⊕	●	●	◑	⊕	●	◑	○	—	○	○	—	—	—	○	⊕	⊕	◑	⊕	⊕	○	○	○	◑	—	—	—	⊕	—
	R	—	○	⊕	○	⊕	⊕	●	⊕	◑	⊕	○	○	○	⊕	○	⊕	⊕	●	○	⊕	○	○	○	○	—	—	⊕	○	○	○	⊕	⊕
RHIZOSOLENIA ALATA	C	⊕	⊕	●	◑	⊕	○	○	●	⊕	◑	◑	◑	—	⊕	—	⊕	○	●	●	●	◑	◑	◑	⊕	○	○	—	○	○	○	○	○
	B	⊕	○	⊕	○	⊕	●	●	◑	⊕	⊕	⊕	—	⊕	○	—	—	—	○	◑	○	○	⊕	◑	○	○	○	○	—	—	—	○	—
	R	—	○	○	○	○	○	○	○	⊕	⊕	⊕	○	○	○	○	○	○	○	○	○	○	○	○	○	—	—	○	○	○	○	○	○
RHIZOSOLENIA H. SEMISPINA	C	○	○	◑	⊕	⊕	⊕	⊕	◑	●	⊕	○	○	—	⊕	—	⊕	●	○	○	○	⊕	○	○	○	⊕	◑	—	◑	●	◑	◑	◑
	B	○	○	⊕	⊕	◑	⊕	○	⊕	◑	◑	○	—	○	◑	—	—	—	⊕	◑	●	○	○	⊕	○	○	○	⊕	—	—	—	●	—
	R	—	○	○	○	○	⊕	○	○	⊕	○	○	○	○	○	○	⊕	◑	○	⊕	○	○	○	○	○	—	—	⊕	⊕	⊕	○	⊕	⊕
HYALOCHAETES	C	◑	◑	●	◑	◑	○	○	◑	○	◑	◑	◑	—	⊕	—	⊕	◑	⊕	⊕	○	◑	●	⊕	○	○	⊕	—	◑	○	◑	○	○
	B	◑	⊕	●	●	●	⊕	◑	○	●	●	◑	—	⊕	⊕	—	—	—	⊕	⊕	⊕	◑	⊕	◑	⊕	○	⊕	◑	—	—	—	○	—
	R	—	⊕	○	○	○	●	○	◑	●	●	⊕	○	○	◑	○	○	◑	⊕	○	○	⊕	○	○	○	—	—	⊕	⊕	⊕	○	○	○
PHAEOCERIDS	C	○	○	●	●	●	●	●	◑	●	◑	◑	◑	—	◑	—	◑	◑	⊕	◑	○	⊕	◑	◑	○	⊕	◑	—	●	●	●	●	○
	B	⊕	⊕	⊕	●	●	●	●	⊕	◑	◑	◑	—	⊕	◑	—	—	—	◑	◑	⊕	◑	⊕	⊕	○	⊕	◑	⊕	—	—	—	◑	—
	R	—	◑	◑	○	○	⊕	⊕	◑	◑	◑	⊕	○	○	○	○	⊕	◑	⊕	◑	◑	○	⊕	⊕	○	—	—	⊕	◑	⊕	⊕	○	○

TEXT-FIG. 4.—Diagrammatic tables, for comparison with Text-figs. 8 and 9 of 'Bulletin' No. 3 (1932–37), showing the varying densities attained by the more important diatoms other than *Rhizosolenia styliformis* and *Biddulphia sinensis* on the three lines from Hull to Bremen, Rotterdam and Copenhagen, month by month from January, 1937, to August, 1939. The months are indicated by the letters J., F., M., etc. One observation is given for each month in which a record was taken: ○ = none found, ⊕ = presence, ◑ = medium patch, = ● major patch, and — = no record taken (see p. 40). Reference to the serial maps in Plates VI to XXXVIII will indicate both the extent of the patches and which lines were sampled in any month. The tables are further continued in Text-fig. 5.

DIATOMS	LINE	1937												1938												1939							
		J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A
BIDDULPHIA REGIA., ETC.	C	⊕	⊕	⊕	⊕	⊕	○	○	○	⊕	○	⊕	⊕	—	⊕	—	○	⊕	○	○	⊕	○	⊕	○	○	○	⊕	—	⊕	○	○	○	⊕
	B	⊕	⊕	●	◑	⊕	⊕	⊕	⊕	◑	◑	⊕	—	⊕	⊕	—	—	—	⊕	⊕	○	⊕	⊕	⊕	⊕	⊕	⊕	◑	—	—	—	⊕	—
	R	—	⊕	◑	⊕	⊕	⊕	⊕	⊕	⊕	◑	⊕	⊕	○	⊕	⊕	⊕	⊕	⊕	○	○	⊕	⊕	⊕	⊕	—	—	⊕	⊕	⊕	⊕	⊕	⊕
BIDDULPHIA AURITA	C	○	○	⊕	○	○	○	○	○	○	○	○	○	—	⊕	—	○	○	○	○	○	○	○	○	○	⊕	⊕	—	○	○	○	○	○
	B	◑	●	●	○	○	○	○	○	○	○	○	—	○	⊕	—	—	—	○	○	○	○	○	○	○	⊕	●	●	—	—	—	○	—
	R	—	⊕	○	⊕	○	○	○	○	○	○	○	○	○	○	⊕	○	○	○	○	○	○	○	○	○	—	—	⊕	○	○	○	○	○
BELLAROCHEA MALLEUS	C	○	○	○	○	○	○	○	○	⊕	○	○	○	—	○	—	○	○	○	○	○	○	⊕	○	○	○	○	—	○	○	○	○	○
	B	⊕	○	⊕	○	⊕	⊕	○	⊕	●	⊕	⊕	—	○	⊕	—	—	—	⊕	○	⊕	⊕	⊕	⊕	○	○	⊕	○	—	—	—	○	—
	R	—	○	○	○	○	○	⊕	●	●	⊕	⊕	○	○	○	○	○	○	○	⊕	⊕	⊕	⊕	○	○	—	—	○	○	○	○	○	⊕
DITYLIUM BRIGHTWELLI	C	⊕	⊕	⊕	⊕	⊕	○	○	○	○	○	○	⊕	—	⊕	—	○	○	○	○	○	○	⊕	○	○	○	○	—	⊕	○	○	○	○
	B	○	⊕	◑	○	⊕	⊕	○	○	○	◑	○	—	⊕	⊕	—	—	—	⊕	○	○	⊕	⊕	⊕	○	○	⊕	◑	—	—	—	○	—
	R	—	⊕	⊕	○	⊕	⊕	○	○	⊕	⊕	○	○	○	⊕	○	⊕	⊕	⊕	○	○	⊕	○	⊕	○	—	—	⊕	○	○	○	○	○
EUCAMPIA ZOODIACUS	C	○	⊕	⊕	◑	◑	○	○	⊕	⊕	○	⊕	⊕	—	⊕	—	⊕	○	○	○	○	○	○	○	○	○	○	—	○	○	○	○	○
	B	○	○	○	○	⊕	○	○	⊕	◑	◑	⊕	—	○	⊕	—	—	—	⊕	⊕	○	⊕	○	○	○	○	○	○	—	—	—	○	—
	R	—	○	⊕	○	⊕	○	○	⊕	○	○	○	○	○	○	○	⊕	⊕	○	○	○	○	○	○	○	—	—	○	⊕	○	○	○	○
NAVICULA SPP., ETC.	C	○	⊕	⊕	⊕	⊕	○	○	○	⊕	⊕	⊕	○	—	◑	—	○	○	○	⊕	○	○	⊕	○	○	○	◑	—	○	○	○	○	○
	B	○	◑	●	○	○	⊕	○	○	⊕	⊕	⊕	—	⊕	⊕	—	—	—	○	○	○	○	⊕	⊕	⊕	⊕	●	●	—	—	—	○	—
	R	—	●	⊕	○	⊕	◑	○	⊕	⊕	⊕	○	⊕	○	○	⊕	⊕	⊕	○	⊕	○	○	○	○	○	—	—	⊕	○	⊕	○	○	○
ASTERIONELLA JAPONICA	C	○	⊕	⊕	◑	◑	○	○	○	○	○	⊕	◑	—	◑	—	○	○	○	○	○	○	⊕	○	○	○	⊕	—	◑	○	○	○	○
	B	○	○	●	◑	●	◑	○	○	○	◑	○	—	⊕	◑	—	—	—	○	○	○	⊕	○	◑	⊕	◑	●	●	—	—	—	○	—
	R	—	●	⊕	○	◑	●	○	◑	●	○	○	○	○	○	○	○	○	○	○	⊕	⊕	⊕	○	○	—	—	○	○	●	●	○	◑
THALASSIOTHRIX NITZSCHIOIDES	C	⊕	⊕	●	●	●	⊕	○	○	○	⊕	◑	●	—	⊕	—	○	○	○	○	○	○	○	○	○	○	◑	—	◑	○	○	○	○
	B	⊕	◑	●	○	●	○	○	⊕	⊕	◑	○	—	◑	⊕	—	—	—	○	○	⊕	○	○	⊕	○	○	●	●	—	—	—	○	—
	R	—	◑	●	○	◑	⊕	⊕	⊕	○	⊕	⊕	⊕	○	⊕	○	○	○	○	○	○	○	○	○	○	—	—	⊕	○	○	○	○	○
GYROSIGMA SPP.	C	○	⊕	⊕	⊕	⊕	○	○	○	○	○	⊕	⊕	—	⊕	—	○	⊕	○	○	⊕	○	○	○	○	○	○	—	○	○	○	○	○
	B	○	⊕	⊕	○	⊕	⊕	⊕	⊕	⊕	⊕	⊕	—	○	⊕	—	—	—	⊕	○	○	⊕	⊕	⊕	○	○	⊕	○	—	—	—	○	—
	R	—	⊕	⊕	○	⊕	⊕	○	⊕	⊕	○	○	○	○	○	○	○	○	⊕	○	○	○	○	○	○	—	—	○	○	○	○	○	○
BACILLARIA PARADOXA	C	○	○	○	○	○	○	○	○	○	○	○	○	—	○	—	○	○	○	○	○	⊕	⊕	○	○	⊕	○	—	○	○	○	○	○
	B	○	◑	○	○	○	○	⊕	◑	⊕	⊕	○	—	⊕	◑	—	—	—	◑	○	○	⊕	⊕	○	○	⊕	⊕	●	—	—	—	◑	—
	R	—	◑	●	○	◑	◑	◑	○	◑	○	○	○	○	○	○	⊕	○	○	○	⊕	○	⊕	○	○	—	—	◑	⊕	○	○	○	○
NITZSCHIA SPP.	C	○	○	⊕	⊕	⊕	○	○	○	⊕	⊕	⊕	○	—	⊕	—	⊕	○	○	○	○	○	⊕	⊕	○	○	⊕	—	⊕	○	⊕	○	○
	B	○	○	⊕	⊕	⊕	⊕	○	○	⊕	⊕	○	—	⊕	⊕	—	—	—	⊕	○	○	⊕	○	⊕	○	○	○	⊕	—	—	—	○	—
	R	—	⊕	○	○	⊕	⊕	⊕	○	○	⊕	○	○	○	○	○	⊕	⊕	○	○	○	○	○	○	⊕	—	—	⊕	⊕	⊕	⊕	⊕	○

TEXT-FIG. 5.—Continuation of Text-fig. 4.

Biddulphia alternans (Bail.) Van Heurck. (Plate XIX shows the patches of September and October, 1938.)

In addition a trace was also found in May, 1938, on the Rotterdam line, and several in the Southern Bight in November. None were seen in 1939 up to the end of the survey. There was a close association with Bacteriastrum spp. during these months, and the two sets of data suggest the possibility of a movement from the German coast northwards, to which we shall later refer.

Bellarochia malleus (Brightw.) Van Heurck. (Plate XV shows the overall distribution in each year.)

Note the limited distribution. No large patches were found, but in 1938 the bulk occurred in the autumn as usual. Differences between the two years are not really significant since we could not obtain samples in the autumn of 1939, but the more northerly samples found in the earlier months of that year are of interest in view of possible movements after the autumn of 1938.

Cerataulina Bergonii H. Pérag. (Plate XXI shows the large patches of May and June, 1939.)

In addition traces and a few very small patches occurred centrally at other times in both years. There are no comparable patches for May and June, 1938 (*cf.* also *Rhizosolenia faeröense*).

Ditylium Brightwelli (West). (Plate XXXV shows the main features in selected maps.)

Other traces were found in the south-east in May, June and September to November, 1938, and January, February, May and June, 1939, but there were none in the north-west other than those shown. The general distribution should be compared with that for *Biddulphia sinensis* (*cf.* Ostenfeld, 1913, who compared it with his group *B. mobiliensis sens. lat.*).

Eucampia zoodiacus Ehr. (Plate XXXV shows the main features in selected maps.)

There were only scattered traces from June to August, 1938, and October, 1938, to March, 1939, whilst none appeared after May, 1939. Note the decrease on the southern lines after 1936 and 1937 (*cf.* Plates XLI–XLIV in 'Bulletin' No. 3).

"Naviculoids." (Plate XXXVI shows the main features in selected maps.)

This comprises the same group of chain forms (Navicula, Fragillaria, etc.) which appeared in 'Bulletin' No. 3. There were only occasional traces at times other than those shown. They appear to have been more abundant in 1939 as far as the evidence goes.

Asterionella japonica Cleve & Möller. (Plate XXX shows the main features in selected maps.)

In addition to those shown there were small patches during the incompletely recorded March, 1938 and to the south of Aberdeen in June. Other traces and very small patches were found in August, October and December; the last, being off the Outer Dowsing Light, is part of a continuous series from November through to the extensive growth there in February and March, 1939. Those patches found in the Southern Bight in the spring and early summer of 1939 may be related to the earlier series of records ; a small one was still there in August. Note also the persistent patches off the Forth-Tay estuaries. The later appearance of the northern patches is seen in each year. Whilst the general distribution is coastal, the distribution in April, 1939, is of interest since Ostenfeld found that " it is only found in quantities near the land " (1913, p. 410).

Thalassiothrix longissima Cleve & Grun. (Plate XXXIII shows the main features in selected maps.)

Note the unusual scale adopted here for convenience. In addition to those shown, extensive patches were found on the Pentland–Hamburg line in March, 1938. Apparently it was much scarcer in the centre of the area in the spring of 1939, and perhaps more abundant in the north-east. The apparent south-eastern movement in the autumn of 1938 should be noted.

Thalassiothrix Nitzschioides Grun., Van Heurck. (Plate XXXII shows the main features in selected maps.)

It is possible that in the north small quantities of unidentified *Thx. Frauenfeldii* have been included in these samples. Very few traces were found after June in each year. In the north by far the larger quantities appeared in 1939, the widespread patches of March and April being very striking.

Gyrosigma spp. (Plate VI shows all the occurrences along with the data for *Paralia sulcata*.)

This includes all the sigmoid diatoms. Their close association at times with the patches of Paralia may be observed and probably, like Paralia, they are only carried into the upper layers at times of extensive disturbance. They were very scarce in the south after September, 1938, and even earlier in 1938 they were much rarer than in 1937.

Bacillaria paradoxa Gmel., Van Heurck. (Plate XXXVII shows the main features in selected maps.)

Other small patches appeared in the Southern Bight in February and April, 1938, and off the Friesian Is. in May and July, 1939. The appearance of traces in the north-west in 1939 may be associated with a similar occurrence of several other diatoms there in that year. There was a marked decrease in 1938 (and possibly 1939) when compared with 1937 (*cf.* Plates XLIII–XLIV in ' Bulletin ' No. 3).

Nitzschia closterium (Ehr.). (Plate XXIX shows the overall distribution.)

Again (see ' Bulletin ' No. 3) this was most common in the presence of Phaeocystis, both in the south and the north-west (probably due to the clogging effect of the flagellate). It is also found at other times, although clearly there is more chance that it will not be recorded when Phaeocystis is absent. The overall distribution is found to be very extensive both in time and space (it was found in every month except December). It is probable that a proportion of *N. delicatissima* has been included at times with the slenderer types of this species, but this should be small.

Nitzschia seriata Cleve. (Plate XXVII shows the date and position of all the main patches, together with all other records.)

Note its rarity in the southern area and the general changes in position between the first and second parts of 1938.

Other species.

Other species recorded were *Streptotheca thamensis* Shrubs., *Hyalodiscus steliger* Bailey, *Melosira Borreri* Greville, Licmophora spp., *Biddulphia favus* (Ehr.), *Actinoptychus undulatus* (Bail.), and Grammatophora spp. There have been no records during 1938–39 of those other species in Table I of ‘ Bulletin ’ No. 3, which are not mentioned above, but which occurred from time to time during 1932–37. On the other hand we should remember that these were usually only isolated recordings, whilst the scale of working has been decreased during the recent years with the adoption of the ten-mile block system.

Discussion.

Although we hope to deal more fully with the various points reviewed below in a later paper, the present circumstances make it desirable to present some tentative suggestions regarding the more obvious features of the data at this date.

The Data for 1938.

It is evident that we cannot regard the year 1938 as providing a full survey ; unfortunately it was not possible to cover anything like the whole area in some months (*e. g.* March), and so important information has been missed. Similarly although the period July, 1938, to June, 1939, for example, was fairly well sampled, there are good reasons for believing that it could hardly be representative in view of various signs that it was a transition period. Yet since this is the first attempt to show monthly pictures of the varying diatom flowerings over the greater part of the North Sea, it may be useful to try to sketch an outline of the general development, and for this purpose it is best to study 1938 as far as the evidence goes.

All the records for January and some for February show the phytoplankton to be very scarce, although a few species show residues of the previous year's growth (*e. g. B. sinensis* and some of the Ceratium spp.). Some however, in February, appear to be initiating a spring flowering ; such were the early diatoms Thalassiosira spp. (at first mainly *Th. decipiens*), Asterionella, some Phaeocerids, Skeletonema and *Thx. longissima.* Appearing first as scattered patches over the Dogger Bank and to the north of it, most of them seem to have developed rapidly in March, giving rise in April to quite extensive patches in the centre of the area. These are dominated by Thalassiosira spp. (now mainly *Th. gravida* and *Th. Nordenskiöldii* along with Coscinosira spp.), chaetocerids of all three groups, *Thx. Nitzschioides* and smaller numbers of Asterionella and Skeletonema. Meanwhile *Thx. longissima* decreased whilst Eucampia, *R. semispina* and *R. alata* had been developing in the central region (just as in the Heligoland Bight the earlier patch of Coscinodiscus spp. had given place to *B. aurita*, and *B. sinensis* showed further growth in the Southern Bight). As far as the incomplete evidence goes there is reason to believe that a similar process went on in the north about one month later, to include a significant patch of *R. styliformis* in May, although apparently not including Eucampia and *B. aurita* or Coscinodiscus spp.

To anticipate a later report we should note here that in April the southern growths of the flagellate Phaeocystis had begun (culminating in May and June), whilst the Dinoflagellates began to appear in appreciable numbers, attaining a maximum much later. There were two initial centres for the production of both groups, as with the diatoms, broadly speaking in the south-east and the north-west. Once again, it seemed, the northern one was about a month behind the southern.

It is necessary to bear in mind the growths of the flagellates, since they play their part in the rapid changes occurring after April. In May the diatoms were generally scarcer in the south (we should note the temporary maximum of *B. sinensis*), although it is likely that they attained their northern maximum then. It is striking that on the whole they were more on the periphery of a central zone which many of them had been occupying before. Just as May shows the rapid development of the flagellate (and, indeed, the animal) plankton, so it proved to be in the nature of a transition month for the diatoms. Few of the earlier ones were left in June, and these were mainly restricted in extent. We may note particularly that whilst *R. styliformis* and *R. semispina* had been decreasing, *R. alata* had become much more prominent, and well-defined patches of *R. Shrubsolei* had appeared in the south-east along with *R. Stolterfothii.* These three last, as well as local patches of *R. semispina*, chaetocerids, Thalassiosira and Skeletonema form a background to the conditions up to September (amongst other details there were relatively large patches of Leptocylindrus). Whilst *R. alata* was most prominent in the northern and central waters, the other two were mainly south-eastern, and in September we see them giving place to the now familiar patches of *B. sinensis*, which have appeared there during each autumn of this survey (in association with various smaller diatoms). At the same time *R. styliformis* appeared over the western patch of the Dogger Bank. In the north-west we find the smaller Rhizosolenias persisting until October, until *styliformis* began to develop there too (though not in association with *B. sinensis*). Other diatoms of the southern autumnal flowering were usually in smaller numbers as far as these records are concerned ; Chaetocerids were prominent, whilst there were smaller patches of Thalassiosira, Leptocylindrus and Skeletonema with fair growths of Coscinodiscus in November. Although in small numbers, it is useful to remember the patches of *B. alternans*, *R. calcar-avis* and Bacteriastrum off the Dutch-German-Danish coasts at this time, and their apparent movements. We should also note the apparent movement of diatoms away from the Scottish coast during the last three months, along with a similar translation shown by the southern patches of *R. styliformis* and *B. sinensis* towards the north-east. By December there was little but *B. sinensis* and small numbers of *C. concinnus* to be found.

The Data for 1939.

In the broadest sense the development in 1939 may be said to have been similar. In fact, the process outlined above is a familiar one, apart from some details which are now available from monthly surveys. On the other hand there are many important differences. Once again the north-western flora tended to be about a month later, and the more numerous spring records for this year enable us to be more certain of this. Very few diatoms were seen in January, but in February early spring forms again appeared, although with a difference in distribution (*e. g. B. sinensis* was restricted to the Borkum region in February instead of near the Outer Dowsing Light, and it had a more northerly position in March and April). It is impossible to compare adequately the conditions in March, although the data for 1939 tend to confirm our earlier suggestion that there had been little growth in the north-west then, when elsewhere the diatoms may be quite abundant. In particular we should note the good growth in the north-east at this time. In April, on the other hand, they were well advanced in the north-west and the data for the spring period show many differences from 1938. Whilst the general background was the same, we may note the general scarcity of, *e. g.*, Eucampia, *R. alata* and *R. Shrubsolei* in 1939, and the lower numbers of *Thx. longissima*, whilst *Thx. Nitzschioides*, Thalassiosira spp., Bacillaria, "Naviculoids," Ditylium and *B. regia* are much more abundant. A number of diatoms appear to be much more northerly this year (or at least scarcer in the south), and amongst these *Thx. longissima* is striking. In particular we must note the patches of *B. sinensis* (along with *B. regia*, Lauderia and traces of Ditylium and Coscinodiscus) in the north-west, and the subsequent patches of Cerataulina and *R. faeröense* (also the slightly more southerly and later traces of Bacillaria), all of which were scarcely (or not) apparent in 1938. In general the northern and north-western complex was much denser, and even in August showed differences from the previous year's growth (*cf.* the patch of Corethron). There were also differences in the distribution of the Ceratia, which will be referred to in a later paper.

There are other differences in the Southern Bight. Whilst a few of the earlier forms were quite abundant at first (*e. g.* Thalassiosira spp.), many were much scarcer (*cf. R. alata*, which was both scarcer and later this year), and on the whole the chief concentrations were more northern (*e. g. R. styliformis*, *R. Shrubsolei*, *R. semispina* and the Phaeocerids). Not until August did *R. alata* attain anything like the densities of the previous year, and along with this we see the general scarcity of *R. Stolterfothii* and Leptocylindrus. Yet a few diatoms, amongst which Asterionella, *B. regia*, Ditylium and Bacillaria stand out, were particularly abundant or persistent. The general impression appears that although the "residual" crop south of the Dogger Bank may at first have been of the order of that in 1938, it became progressively thinner and, indeed, the area affected in this way became larger. In association we may anticipate the flagellate data to say that whilst Phaeocystis was perhaps even denser than in 1938, all the species of Ceratium were fewer in the southern half of the area.

During the year 1938 and the incompletely sampled 1939 it is worthy of note that, after a period in which the diatoms were fairly widespread over the central waters of the North Sea, they became progressively scarcer there from May onwards, the summer patches being on the whole much more coastal and, of course, thinner. This is more striking in 1938 than 1939, perhaps owing to the smaller numbers in the south for the latter year, and we see that it was not until October and November that they became relatively significant in the central waters again.

Comparison with the Data for 1932–37.

The differences seen here could be understood better in relation to a longer period. Unfortunately there are no adequate data for the northern area, but the more southern data may be compared with that in 'Bulletin' No. 3. There we came to the conclusion that over the period 1932 (or 1931) to 1937 there had been a general increase in the densities of the residual crops of diatoms and Dinoflagellates, culminating variously in 1935, 1936 or 1937, although mainly the last. In several ways 1934 and 1936 showed deviations from this trend, and in some species it probably began after 1933, rather than in 1932. By no means all showed the trend, but most did so, and some which did not show the change in numbers still showed changes in distribution which might have been related.

In view of this we awaited the data for the later years with great interest in order to see whether any return to the earlier conditions might be found. Text-fig. 2 shows the total numbers of *R. styliformis* and *B. sinensis* for each record in 1938–39, arranged as in Text-fig. 5 of 'Bulletin' No. 3; for effective comparison the totals are for the shorter lines of the old period (180 miles of the Hull–Bremen route, from the Outer Dowsing Light to Borkum, and for 250 miles from the Humber Light on the Hull–Copenhagen route). *R. styliformis* was much scarcer on the Bremen route in 1938 (and also on the Rotterdam, as far as the slight evidence goes), although it was slightly more abundant on the Copenhagen route for a short period. *B. sinensis* decreased even more extensively on the first and, although along the Copenhagen route it reached a similar quantity, it persisted for a shorter time than in 1938. In association we must note that it extended far less towards the Outer Dowsing Light this year than it had done since 1933; consequently the mixing with *R. styliformis* was slighter. Similarly its extension along the Copenhagen line was limited to the waters east of the Dogger Bank in contrast to the unusual (in these records) extension in 1937. On the other hand the total on the Rotterdam line was much higher than before, and both spring totals were rather higher than before. These points are brought out in Text-fig. 3, which shows the maximal quantities found on the different parts of each line throughout 1937 and 1938; they may be compared with Text-figs. 6 and 7 of ' Bulletin ' No. 3. The lack of samples in 1939 prevents the useful comparison we should have wished to make for another year, but we should note the patch of *R. styliformis* and the traces of *B. sinensis* in July and August which may be the precursors of new autumn patches. As far as the evidence goes, both diatoms appear to have been scarcer in the spring of 1939 than in that of 1938.

So far there is some evidence of a decrease in these forms to which we have paid more attention; this is confirmed by many other diatoms. Owing to the approximations used in some of the earlier work it is not possible to provide strict comparison between the new and the earlier data. However, the patches represented by the larger open circles in Plates XVI to XXXVIII approximately compare with the " medium " patches of earlier years, the higher values comparing with the " major " patches of 1932–37 (it is evident, as we suggested, that we could also have allowed for a " very dense " grade in ' Bulletin ' No. 3: similarly it is now found useful to have the lower grade of the smaller open circles). On this basis Text-figs. 4 and 5 have been prepared to show the data for 1938–39 in comparison with that for 1937, as in Text-figs. 8 and 9 of ' Bulletin ' No. 3. Most of the diatoms provided smaller numbers (viewed thus) in 1938 and/or 1939 than in 1937, the year in which so many had been apparently at their highest. In some the reductions are such that they approach the values of the very scanty early years (*e. g.* Eucampia, *Thx. Nitzschioides*, Bacillaria, *R. Stolterfothii*). The absence of important spring records on the Hull–Bremen line prevents the best comparison, but even allowing for this it appears that only *R. semispina* attained high densities for a significantly longer period in 1939 than in 1937 or 1938. Such a method gives a biased view, and the spatial distribution must also be considered. The absence of certain records (or their incompleteness at times) prevents full comparison, but when this is possible, we see again that most species were scarcer on the whole in the last two years, only the Thalassiosira group and the " Naviculoids " showing significantly more widespread distributions on these lines in 1939. Although much of the present work goes to show how near patches may be to these three lines without actually appearing on them (and so detracting from their value as standards), we should also note that the Esbjerg line (which crosses two of them) was also particularly thinly populated in 1939.

At this stage we may refer once again to the data for the Ceratium spp. Whilst on the Bremen and Rotterdam lines the 1938 totals were even higher than in 1937 (the highest so far on these lines), there was a big reduction on the Copenhagen line. Even more striking were the conditions in 1939, when all the species showed marked reductions for each month in which there were samples. Even on the Rotterdam line the patch of *C. fusus*, which had been so abundant in 1937 and 1938, was insignificant until August, and then was much less than in 1938. The totals for the two northern lines were more of the order of the low values found in the earlier part of the survey. On the other hand, we have found that Phaeocystis, which was abundant in the first years and then scarcer until an increase occurred in 1937, was even more abundant in the last two years.

One more point of comparison is noteworthy. In ‘Bulletin’ No. 3 (p. 132, and Text-fig. 10) we showed how in the earlier years the diatoms tended to be towards the edges of the Dogger Bank, whereas later they became relatively more abundant in the central and western regions of the Copenhagen line. Similarly on the Bremen and Rotterdam lines they tended to become more western in distribution. In 1938, however, the patches were on the whole much scarcer in the western waters (particularly those round the Humber mouth and on the western half of the Rotterdam line). Once again we see that, although the 1938–39 diatoms were often more abundant than in the earliest years, yet in still another feature they resembled these rather more than 1936 and 1937.

In comparison with Ostenfeld’s Plankton Resumé (1931) it is evident that, in general, both these results and those of the quarterly surveys of the International Council are in agreement for the southern and the northern North Sea. On the other hand the monthly data usually available here enables one to denote the periods of maximum with much greater precision than before. As a point of disagreement we may note that *Rhizosolenia h. semispina* is omitted from Ostenfeld’s list of common spring forms in the southern and the northern North Sea; it is also surprising that *Thalassiosira* spp. does not appear there as a spring form for the southern North Sea and *Biddulphia sinensis* in the autumn. The last may well be due to the fact that *B. sinensis* was only then (1902–08) beginning to develop in the area, but throughout this work all three have appeared as important diatoms in the phytoplankton, even after allowing for their various sizes in relation to those of the other species.

We cannot make similar comparisons for the northern waters, except to emphasize the changes from 1938 to 1939, the general increase in the last year providing a complement to the reductions in the south. It seems important to emphasize also the occurrence of a number of forms there in 1939 which we did not find so abundantly (or at all) in 1938, some being more (or entirely) restricted to the southern waters in 1938. Although in March and April there is unfortunately a shortage of records here in 1938, wherever comparison can be made the difference is quite sharp (*cf.* the later differences for May–August, in which most of the records are available). There seems to have been a distinct addition to the flora, since most of those present in 1938 were also there in 1939. We may note that for one of the diatoms, *B. sinensis*, the Scottish records suggest that not since 1930 has it been so abundant there (p. 31). It seems very unfortunate that owing to the war the records should have ceased; there is reason to believe that data even for one or two more months might have added largely to our knowledge of the apparent cycle of events in the North Sea during the last few years—particularly regarding the autumnal flowerings of *R. styliformis* and *B. sinensis* in the Southern Bight.

General Remarks.

Whilst we had to limit our work at first to three divergent lines from Hull, we had the difficulty of being uncertain how applicable the data might be to the problems for solution. The Esbjerg line immediately gave some checks on this, and we could see how on the whole the data from the intersecting lines was confirmatory. Yet we often had evidence that the absence of an organism from the Bremen line, for example, could be misleading, since it might be found in fair numbers on the other (see ' Bulletin ' No. 3, p. 100). Now that we have had ten lines, each normally intersecting with another at least once in each month, it is clear that the individual lines can only be used with qualification. There are still large gaps in the network in which important processes may go on undetected (the results from the unusual recording of a Lerwick–Hamburg line in July, 1939, may be noted here). The whole set of records must be associated and full allowance made for the gaps in observation, both in time and space, and the varying times of recording.

In this connection the new work has provided even more evidence of the importance of patchiness (and more reliable data for its study in some species). Whilst the more general remarks of the earlier survey will still apply, they require qualification. When we consider the diatoms as a group, we see at first very marked patches with sharp boundaries, yet within these general patches are equally sharply defined sub-patches of the individual species (or even varieties). Data for the Dinoflagellates present similar features. In general (and this applies by no means only to the phytoplankton) we see that there are regions which are productive for one of the main groups, which may yet yield very different analyses within their boundaries ; the time factor shows this to be a dynamic problem, and one which concerns the inter-relationships of different organisms, both physical and biological (see also Lucas, 1938). It seems likely that many of the details, and perhaps some of the broader features, of annual and even longer cycles will be bound up with this problem.

The data from this and the earlier survey are already being studied in relation to the hydrology of the North Sea and water movements ; certain features can only be understood in this light. Both 1938 and 1939 have shown further evidence of the type of movement suggested for the south in earlier years, although 1939 shows also some obvious differences. However, the extension which has enabled us to link the old area to a much wider field is likely, through the information gained in the north, to produce a better understanding of the southern events. Examples are seen in the apparent translation of many forms (*Thx. longissima*, *R. styliformis*, Dactyliosolen and the Chaetocerids) away from the Scottish coast eastwards and southwards in the autumn of 1938; with this we may associate the more familiar movements in the south-east as *R. styliformis* and *B. sinensis* recede towards and along the Dogger Bank (although the latter does not, as in 1937, spread over the western half of the Dogger Bank). Patches of Chaetocerids and the smaller Rhizosolenia spp. appear to be moving in the same manner, whilst some zooplankton species show similar changes. On the other hand the relative stability of some patches in time suggests, not so much a lack of movement, as the persistence of suitable conditions (perhaps from swirls or upwelling) in that region. Such are found, for example, near the western and eastern ends of the Dogger Bank, particularly in the autumn, and off the coast of Scotland on a number of occasions (in particular the possibly continuous occurrence of a patch of Asterionella in the Southern Bight from November, 1938, to August, 1939, may be the results of some such swirl (see p. 34). The more or less regular occurrence of such concentrations of diatoms and their detailed variations in position must be of great significance in consideration of the bottom communities of these regions (*cf.* Orton, 1937, on the relations between swirls or eddies and the local ground fauna).

In addition to such hydrological evidence as is provided by the movements or persistence of " bodies " of diatoms (relatively persistent communities which can be identified from time to time), we have also been using the method of identification adopted by Wimpenny (1936)—that of measuring cell sizes. As well as measuring the sizes of cells of suitable *R. styliformis* patches in 1932–37, at least some measurements have been made in all the patches of 1938–39. These will provide material for a paper to follow, but we may anticipate results to say that the data suggest a ready means of separating the northern and the southern crops during these years. On the whole the northern cells were much smaller, and the general difference might seem to imply a mixing of the two crops in the central North Sea towards the end of 1938. Plate VII provides a summary of the data for 1938 by showing symbolically the sizes of the *smallest* cells found throughout the whole year on each pair of blocks (" double " blocks of twenty miles). In this way the black symbols (denoting the larger " smallest " cells) show clearly a south-eastern region in which cells similar to the even smaller ones of the north-west were rarely recorded. Along the northern edge of this area there appears to be a region in which the two smallest sizes are mixed. The relationships between these are complex and will be discussed in the later paper. Meanwhile the problem is also being investigated by Mr. R. S. Wimpenny (of the Ministry of Agriculture and Fisheries' Laboratory at Lowestoft), with whom the writer is in touch; it is hoped that through these different approaches a sound solution will be found for this interesting distribution. It seems likely that such work might profitably be extended to some other species, and since the Recorder material has certain advantages for this purpose (as well as some disadvantages), we are continuing the investigation by means of analyses of the sizes of *B. sinensis* which are likely to have a rather different relevance.

A few concluding remarks should be made regarding the incomplete cycle of events which we have postulated for the period 1932–39. Full consideration must be deferred until the data for the zooplankton can be reviewed as well as the associated conditions in the sea, although we may say that some similar trends have also been found in the zooplankton. However, it is suggested that the " residual stock " of many phytoplankton species appeared to increase for some years (variously from 1931–33 to 1935–37), and that thereafter they decreased to various extents. In association one or two species appeared to do the reverse, or showed more or less cyclic changes in time and space. We referred in 'Bulletin' No. 3, p. 164, to other changes which were observed by other writers in the earlier period : *e. g.* the occurrence of Sagitta spp., young fish, phosphates and phytoplankton in the English Channel and the varying northern influences on the North Sea. Very tentatively it was suggested that the increased phytoplankton in the southern North Sea might be due to increased phosphate supplies arising from the unusual water movements there (with perhaps some lag period between them, *cf.* Russell, 1939, p. 184), just as off Plymouth the reverse seems to have occurred. On such a suggestion the recent decreases might well be due to a decrease in phosphate as the " abnormal " conditions disappeared, probably with a lag period.

Whilst this possibility will be more fully examined later, it is important to mention some evidence which offers partial confirmation for the suggestion. Dr. Carruthers has examined the varying rates of water-flow past the Varne Lightvessel since 1926, and found fairly strong rates of flow into the North Sea on the whole up to 1931. Then he found a varying amount of " hold-up " or " reversal " (Carruthers' terms) of the flow up to and including 1937 (Carruthers, 1935, and Min. of Agric. and Fish., Reports on Sea Fisheries for 1935–37). We are greatly indebted to him for permission to make use of his latest unpublished data. This shows that after the beginning of 1938 a strong flow to the North Sea again set in, and persisted with little interruption until the end of these observations in August, 1939. Such a persistent flow had not been recorded since 1930, and even before that there had been none of such a steady nature. During these years there has been, in fact, a cycle (more or less irregular) in the pressure balance between the North Sea and the English Channel.

The links between these different events are by no means clear as yet, though the data for the last two years help to carry us a step further. It will be unwise to look too deeply without the necessary zoological and hydrological evidence, but it seems fair to point out that if, after a long period when the Channel waters were deficient in phosphate, they begin to flow again into the Southern North Sea in (relatively) unusual quantity, then it is not so surprising that the phytoplankton resulting in that area should be poorer. It will be remembered that whilst some of the earlier species of 1938 and 1939 were fairly abundant, the greater decreases were seen in the autumn of 1938 and the later spring and summer of 1939, as if the available phosphates were being used up, *or being swept out of the area.* Judging from the biological evidence it seems possible that the processes in the southern

North Sea may be returning to conditions not so dissimilar from ones seen in the earlier years of the survey. Such a return would have important corollaries for other events in that area, and it is also tempting to wonder if the trends which have occurred in the English Channel region will soon be directed back towards earlier conditions. Up to date Russell (1939) has not been able to report any sign of such a return. On the other hand, the Report of the Scottish Fishery Board for 1938 mentions that "the sea water conditions . . . would appear to have become more or less normal after a long period cycle of abnormalities in the northern North Sea." The various pointers seem to be directed towards the same conclusions, and it is greatly to be hoped that the war will not result in the cessation of all means of recording whereby we might have some knowledge of the contemporary changes.

SUMMARY.

1. The present 'Bulletin' concerns an extension of the earlier survey of the southern North Sea with the Continuous Plankton Recorder to include the central and northern waters. It deals with the changes in composition and distribution of the diatom plankton month by month from January, 1938, to August, 1939. Data for the Dinoflagellates and Phaeocystis will appear later.

2. Six extra steamship lines were run monthly : from Hull to Oslo, from Leith to Hamburg, Copenhagen and Lerwick and from the Pentland Firth to Hamburg and Bergen. The material and methods are described on pp. 19 to 23.

3. Whilst particular attention is still being paid to the diatoms *Rhizosolenia styliformis* and *Biddulphia sinensis* (pp. 28 and 31), a number of other species have been examined and illustrated in more detail than before (pp. 23 to 36).

4. Variations occur in time and space which essentially resemble those of the earlier 'Bulletin'; they are shown in a series of monthly maps for the different species (Plates VI–XXXVIII). From them arise further evidence of "patchiness," "inter-relationships" and of water movements.

5. Standing out from these details are certain general tendencies. The northern diatoms were more abundant in 1939 and the southern ones in 1938. On the whole the southern crops have decreased since the period 1935–37 (pp. 36 to 42).

6. This apparent decrease in the southern North Sea follows the general increase suggested to have occurred between 1932–33 and 1935–37. There appears to have been a cycle of growth in the area, probably in association with certain hydrological changes to which attention is tentatively drawn (pp. 42 to 45). Owing to the onset of the war it has been impossible to obtain further records after August, 1939, and so further stages in this "cycle" cannot now be followed out.

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EXPLANATION OF PLATES VI TO XXXVIII.

PLATE VI.

Maps showing the distribution of *Paralia sulcata* (in line) and Gyrosigma spp. (×) month by month in 1938 and 1939. The thick line denotes that Paralia was common and the thin one that it was scarce or absent. The distribution of Paralia and Gyrosigma is referred to on pp. 23 and 35 respectively.

PLATE VII.

Showing the sizes (in μ) of the " smallest " cells of *Rhizosolenia styliformis* recorded for each block of twenty miles on the normal routes during 1938. Those " smallest " cells per block which were larger than 40μ are denoted by white figures on black. See discussion on p. 43.

PLATES VIII–X.

Maps showing the distribution of *Rhizosolenia styliformis* (p. 28) month by month from January, 1938, to June, 1939. Numerals and symbols are used to denote the varying numbers per mile in each ten-mile block (for scale see inset on Plate IX). Where more than one record has been obtained within any month, they have usually been shown " in parallel " (the earlier one above) and bracketed together. Where this has not been possible, one representative record has been shown in the usual manner and the other(s) have been shown in the margin (as in November, 1938), the symbols I and III denoting the first or the third of the series (for dates see ' Bulletin ' No. 8).

PLATE XI.

Maps showing the continuation of *Rhizosolenia styliformis* for July and August, 1939; also the overall distribution of *Rhizosolenia calcar-avis* (p. 29) and Dactyliosolen spp. (p. 25) in 1938; neither of the latter were recorded in 1939.

PLATES XII–XIV.

Maps showing the distribution of *Biddulphia sinensis* (p. 31) month by month from January, 1938, to June, 1939, arranged in the same manner as those of *R. styliformis* (see explanation of Plates VIII–X above).

PLATE XV.

Maps showing the continuation of *Biddulphia sinensis* for July and August, 1939; also the overall distribution of *Biddulphia mobiliensis* + *B. granulata* (p. 31), *Biddulphia rhombus* (p. 31), *Bellarochia malleus* (p. 34) and *Corethron criophilum* (p. 25) in 1938 and 1939.

PLATES XVI AND XVII.

Maps showing the distribution of *Rhizosolenia alata* (p. 28) month by month from January, 1938, to August, 1939. Symbols are used to denote the varying numbers per mile in each ten-mile block (for scale see inset on Plate XVI). Where more than one record has been obtained in any month, they have usually been shown " in parallel " (the earlier one above) and bracketed together. Where this has not been possible, one representative record has been shown in the usual manner and the other(s) have been shown in the margin (as in August, 1938), the symbol AI denoting the first of the pair (for dates, see ' Bulletin ' No. 8).

The inset on Plate XVII shows the distribution of *Biddulphia regia* (p. 31) in March and April, 1939 (scale, etc., as above), and also the overall distribution in 1938 and 1939.

PLATES XVIII AND XIX.

Maps showing the distribution of *Rhizosolenia shrubsolei* (p. 28) month by month from January, 1939, to August, 1939, arranged in the same manner as those of *R. alata* (see explanation of Plates XVI and XVII above).

The inset on Plate XIX shows the distribution of *Biddulphia alternans* (p. 33) in September and October, 1938 (scale, etc., as above).

PLATES XX AND XXI.

Maps showing the distribution of *Rhizosolenia hebetata semispina* (p. 29) month by month from January, 1938, to August, 1939, arranged in the same manner as those of *R. alata* (see explanation to Plates XVI and XVII above).

The inset on Plate XXI shows the distribution of *Cerataulina Bergonii* (p. 34) in May and June, 1939 (scale, etc., as above).

PLATES XXII AND XXIII.

Maps showing the distribution of Thalassiosira spp. (including Coscinosira spp., p. 24) month by month from January, 1938, to August, 1939, arranged in the same manner as those for *R. alata* (see explanation to Plates XVI and XVII above).

The inset on Plate XXIII shows the distribution of *Rhizosolenia faeröense* and *R. fragillima* (p. 28) in July and August, 1939 (scale, etc., as above).

PLATES XXIV AND XXV.

Maps showing the distribution of Chaetoceros spp. (s.g. Phaeoceros, p. 30) month by month from January, 1938, to August, 1939, arranged in the same manner as those for *R. alata* (see explanation to Plates XVI and XVII above).

The inset on Plate XXV shows the distribution of Bacteriastrum spp. (p. 27) from August to October, 1938 (scale, etc., as above).

PLATES XXVI AND XXVII.

Maps showing the distribution of *Chaetoceros decipiens* (p. 30) month by month from January, 1938, to August, 1939, arranged in the same manner as those for *R. alata* (see explanation to Plates XVI and XVII above).

The inset on Plate XXVII shows the distribution of *Nitzschia seriata* (p. 36) during the periods January to July, 1938, August to December, 1938, and January to August, 1939 (scale, etc., as above). The Roman numerals denote the months in which the patches occurred.

PLATES XXVIII AND XXIX.

Maps showing the distribution of Chaetoceros spp. (s.g. Hyalochaete less *Ch. decipiens*, p. 30) month by month from January, 1938, to August, 1939, arranged in the same manner as those for *R. alata* (see explanation to Plates XVI and XVII above).

The inset on Plate XXIX shows the overall distribution of *Nitzschia closterium* (p. 35), *Stephanopyxis turris* (p. 25) and *Guinardia flaccida* (p. 25) during 1938 and 1939.

PLATE XXX.

Maps showing the distribution of *Asterionella japonica* (p. 34) in 12 selected months during 1938 and 1939, arranged in the same manner as those for *R. alata* (see explanation to Plates XVI and XVII above).

PLATE XXXI.

Maps showing the distribution of *Skeletonema costatum* (p. 24) in 12 selected months during 1938 and 1939, arranged in the same manner as those for *R. alata* except that the scale is slightly modified as shown (see explanation for Plates XVI and XVII above.)

PLATE XXXII.

Maps showing the distribution of *Thalassiothrix Nitzschioides* (p. 35) in 12 selected months during 1938 and 1939, arranged in the same manner as those for *R. alata* (see explanation for Plates XVI and XVII above).

PLATE XXXIII.

Maps showing the distribution of *Thalassiothrix longissima* (p. 35) in 12 selected months during 1938 and 1939, arranged in the same manner as those for *R. alata* except that the scale is modified as shown (see explanation for Plates XVI and XVII above).

PLATE XXXIV.

Maps showing the distribution of *Rhizosolenia Stolterfothii* (p. 28) in 12 selected months during 1938 and 1939, arranged in the same manner as those for *R. alata* (see explanation for Plates XVI and XVII above).

PLATE XXXV.

Maps showing the distribution of *Ditylium Brightwelli* (p. 34) and *Eucampia zoodiacus* (p. 34) in selected months during 1938 and 939, arranged in the same manner as those for *R. alata* (see explanation for Plates XVI and XVII above).

PLATE XXXVI.

Maps showing the distribution of *Biddulphia aurita* (p. 30) and the " Naviculoid " diatoms (p. 34) in 6 selected months during 1938 and 1939, arranged in the same manner ast hose for *R. alata* (see explanation for Plates XVI and XVII above).

PLATE XXXVII.

Maps showing the distribution of *Bacillaria paradoxa* (p. 35) and *Leptocylindrus danicus* (p. 25) during 6 selected periods in 1938 and 1939 (scale, etc., as in Plate XXXVI). The Roman numerals denote the months in which the patches occurred.

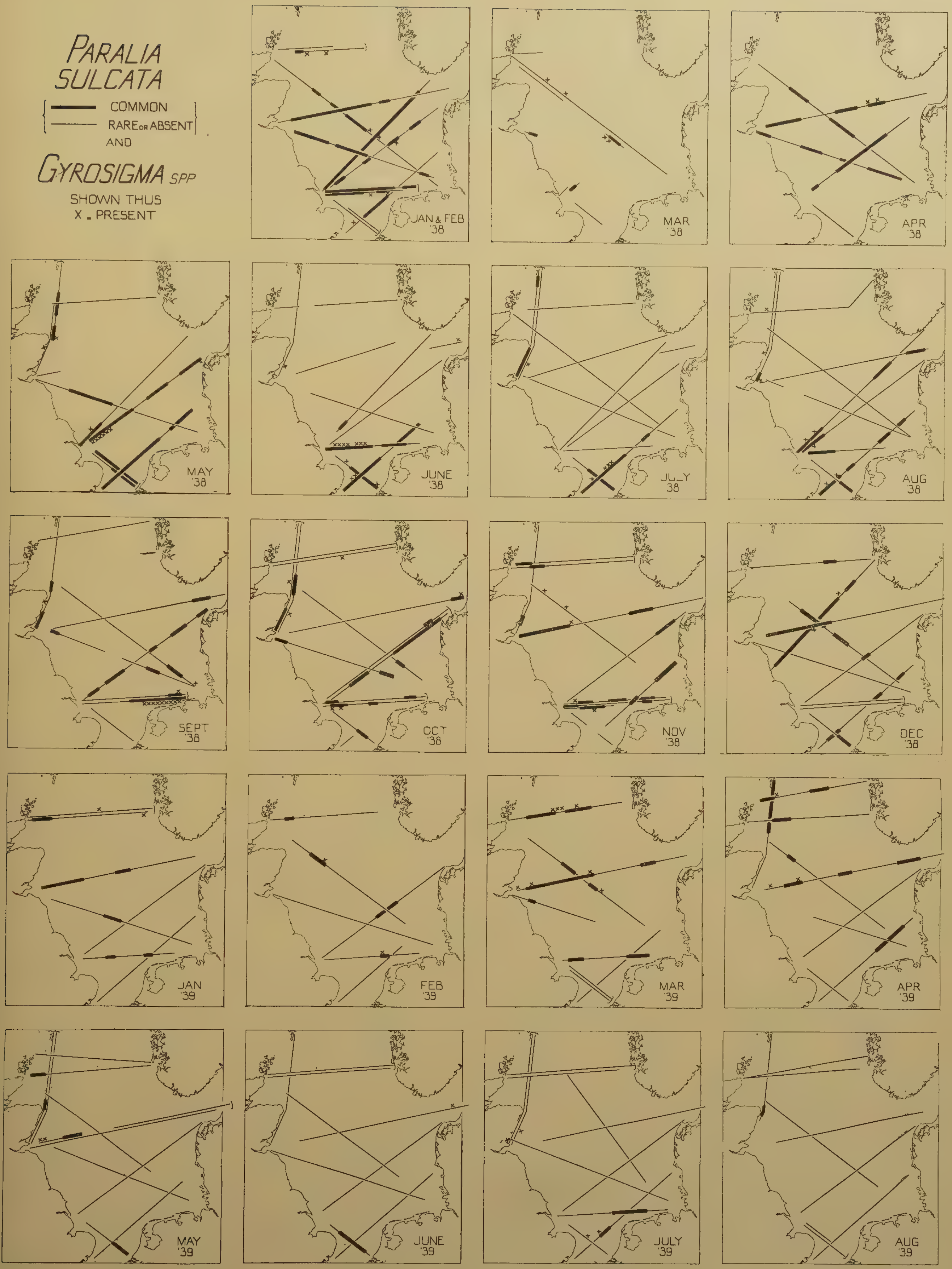
PLATE XXXVIII.

Maps showing the distribution of *Lauderia borealis* (p. 24) and the larger Coscinodiscus spp. (p. 24) during 6 selected periods in 1938 and 1939 (scale, etc., as in Plate XXXVI). The Roman numerals denote the months in which the patches occurred.

Corrigendum.

As the result of an oversight the data for the Pentland–Bergen record of October 22, 1938, has been slightly mis-plotted on each occasion on which it has been used. Instead of being in the direct line, as in the previous record, the direction was changed during the voyage, the true route being as in Plate II of ‘ Bulletin ’ No. 7. For most purposes the error may be regarded as a slight one.

PLATE VI



PARALIA SULCATA

▬ COMMON

— RARE OR ABSENT

AND

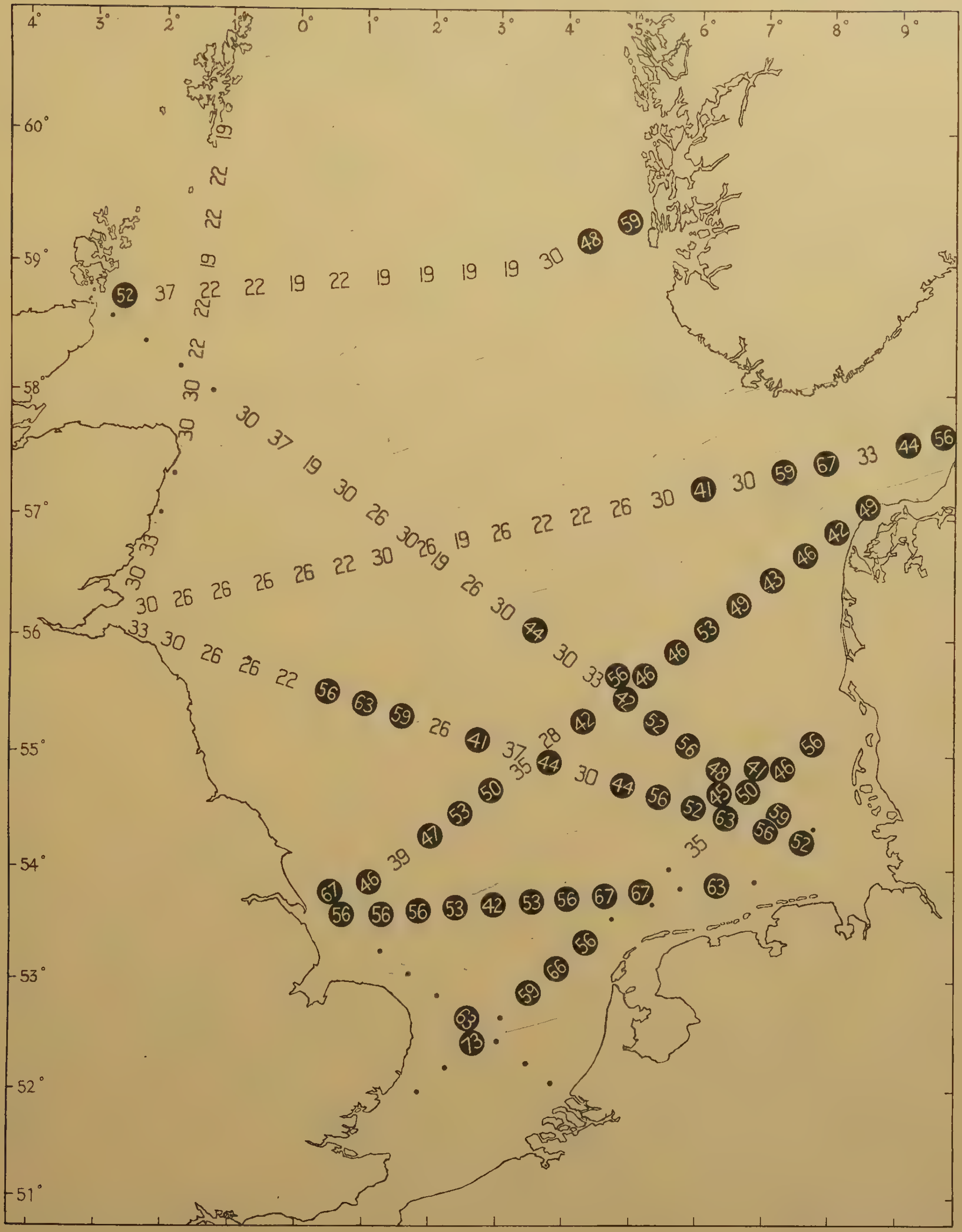
GYROSIGMA SPP

SHOWN THUS

X – PRESENT

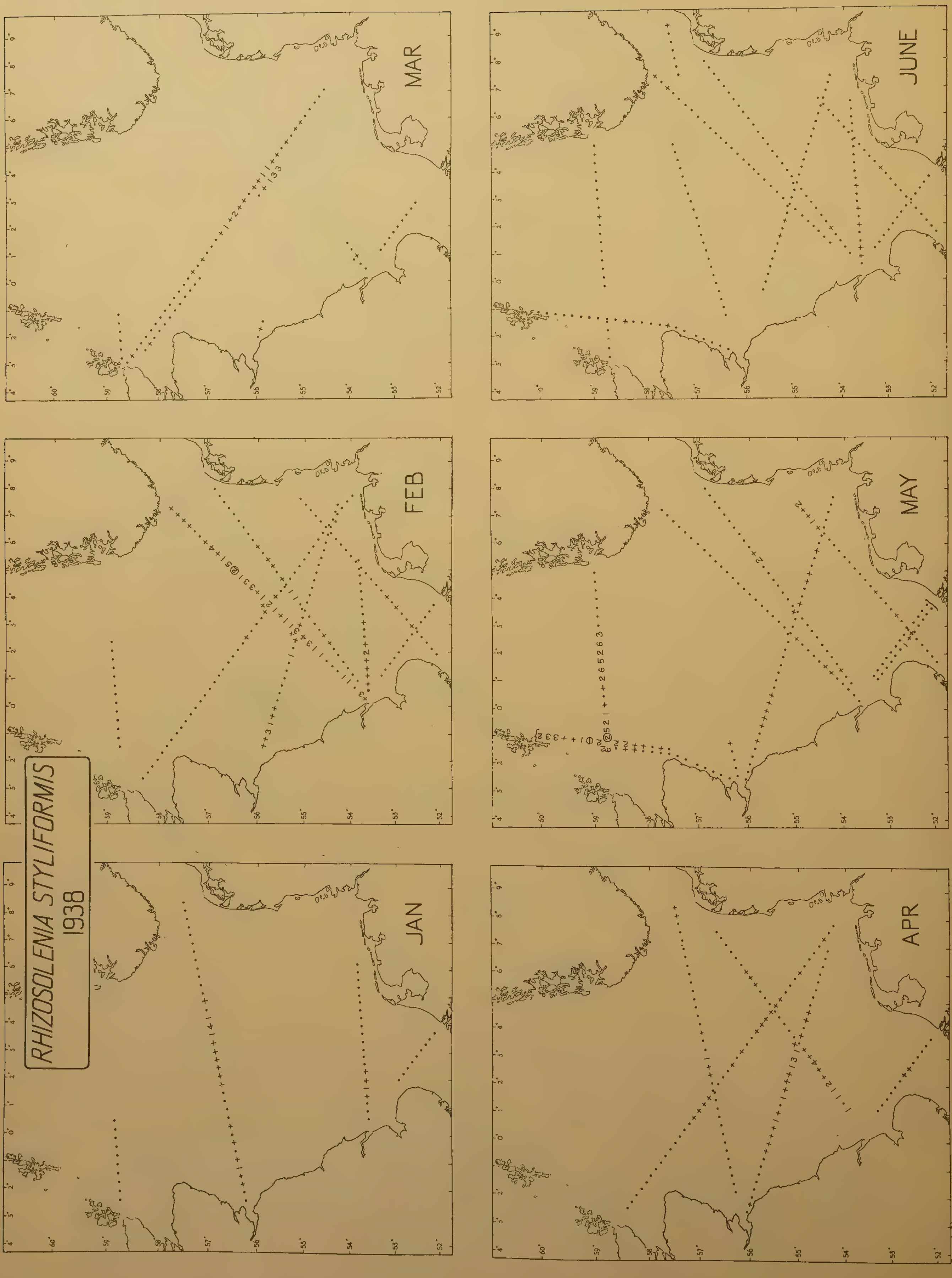
JAN & FEB '38
MAR '38
APR '38
MAY '38
JUNE '38
JULY '38
AUG '38
SEPT '38
OCT '38
NOV '38
DEC '38
JAN '39
FEB '39
MAR '39
APR '39
MAY '39
JUNE '39
JULY '39
AUG '39

PLATE VII



Showing the sizes [in μ] of the smallest cells of *Rhizosolenia styliformis* recorded for each block of twenty miles on the normal routes during 1938. Those larger than 40 μ are denoted by white figures on black.

PLATE VIII



RHIZOSOLENIA STYLIFORMIS
1938

MAR
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7°
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3°
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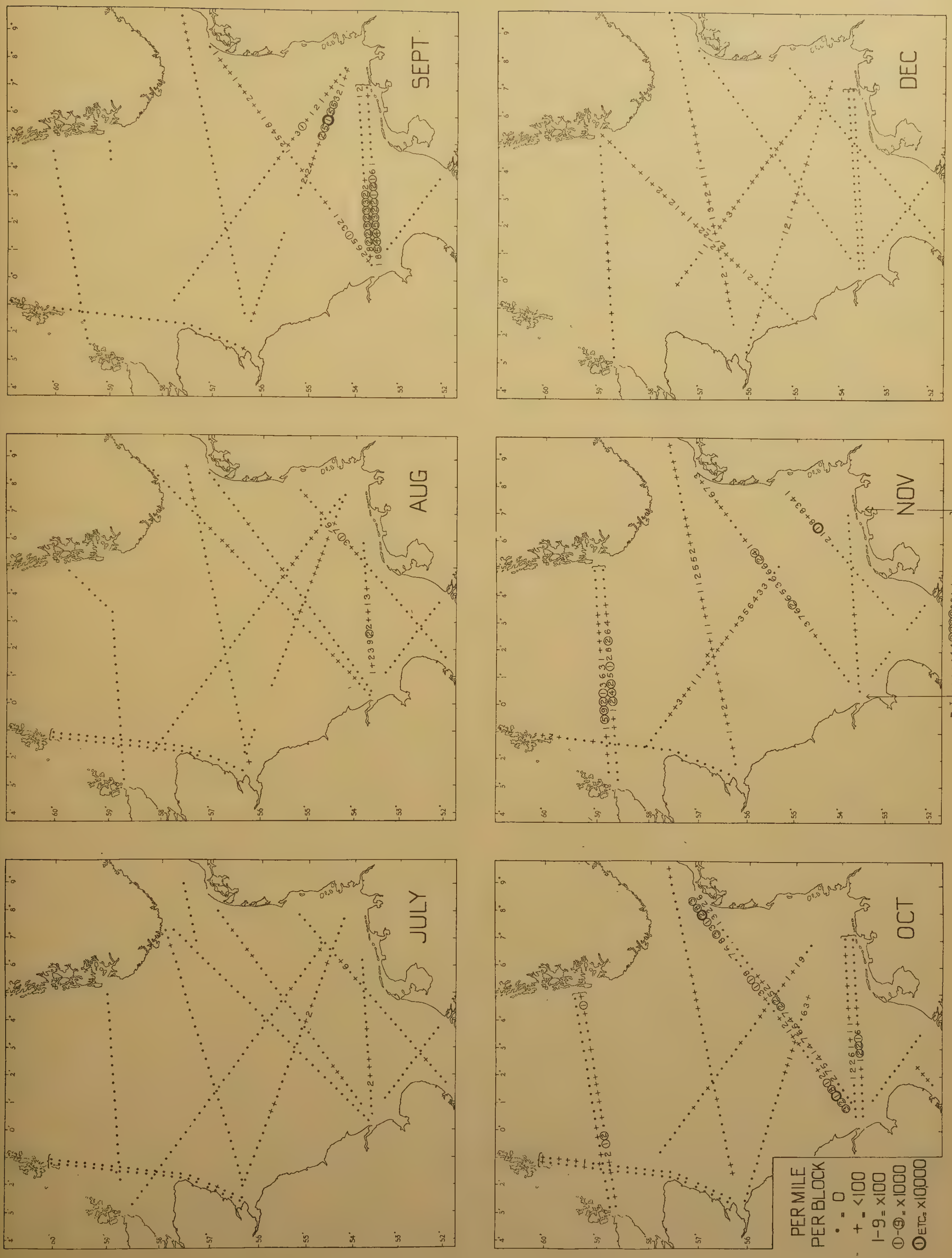
PLATE IX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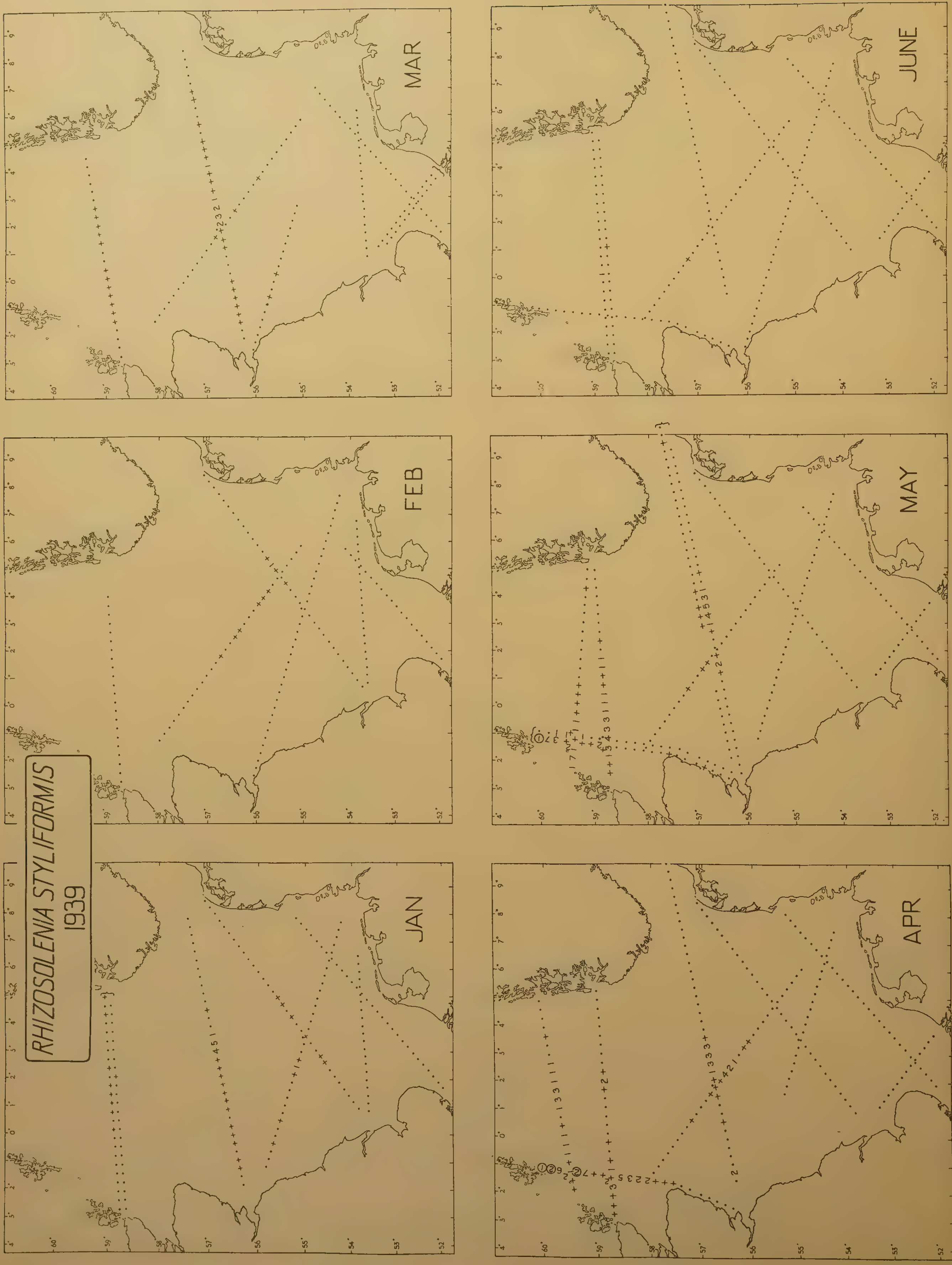
DEC
AUG
NOV
JULY
OCT
B I
B III
PER MILE
PER BLOCK
· = 0
+ = <100
1-9 = x100
①-⑨ = x1000
① ETC = x10,000

PLATE X



RHIZOSOLENIA STYLIFORMIS
1939

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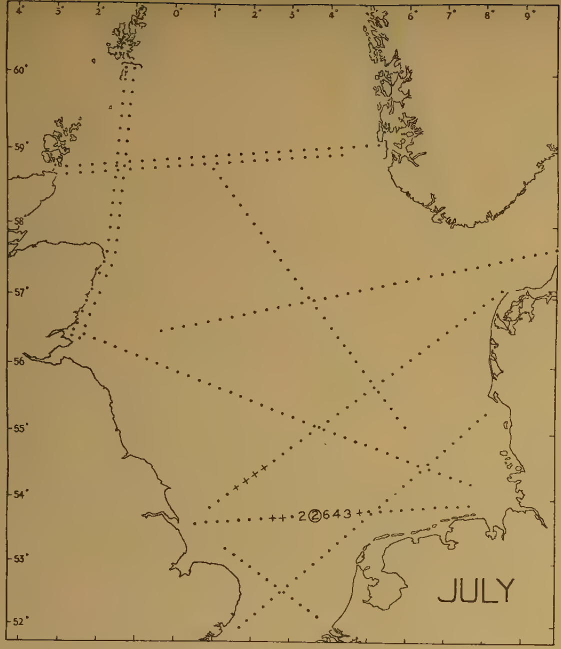
52°

RHIZOSOLENIA STYLIFORMIS
1939 CONTD.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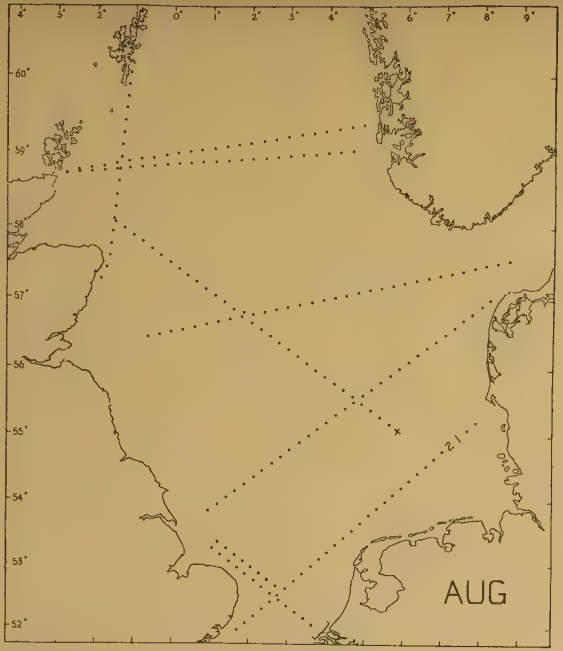
JULY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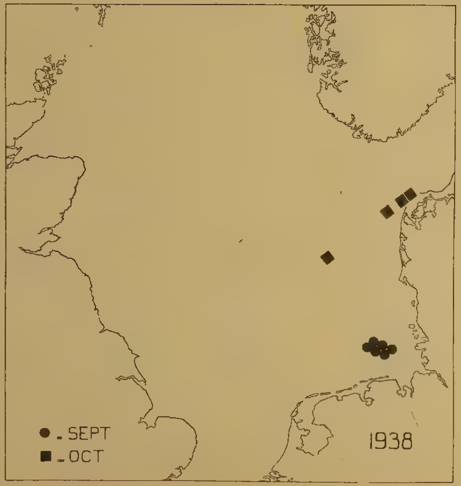
21
AUG

RHIZOSOLENIA CALCAR-AVIS
All records :


● - SEPT
■ - OCT
1938

DACTYLIOSOLEN SPP.
All records :

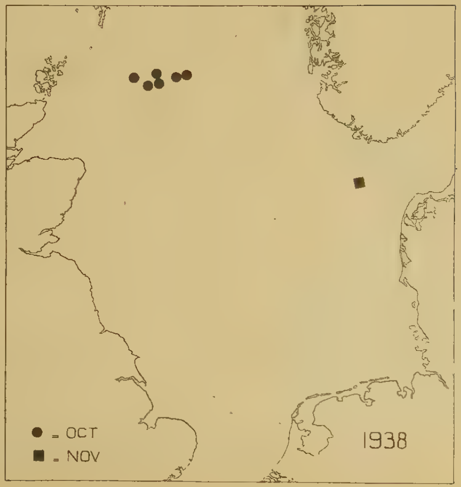
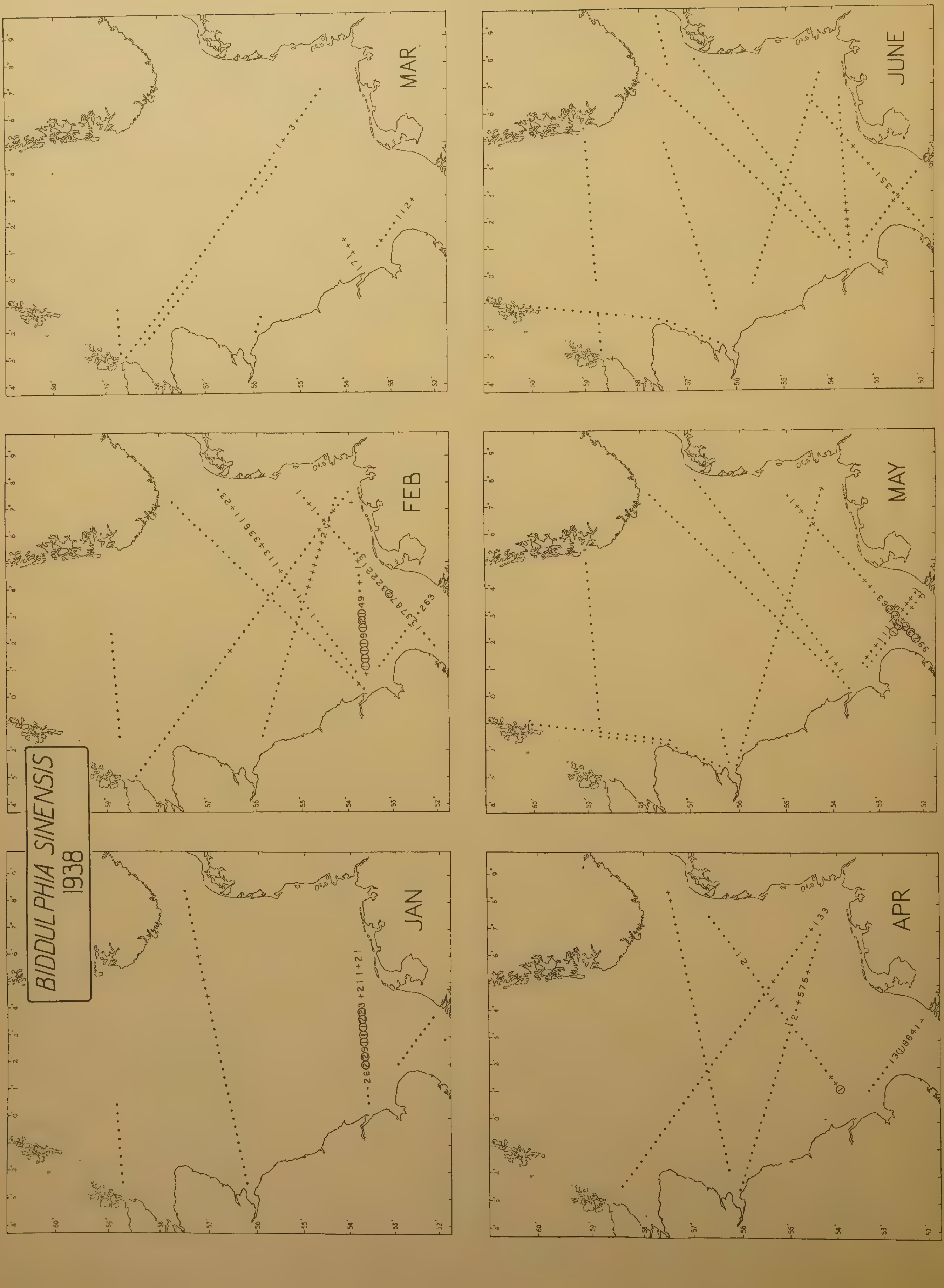
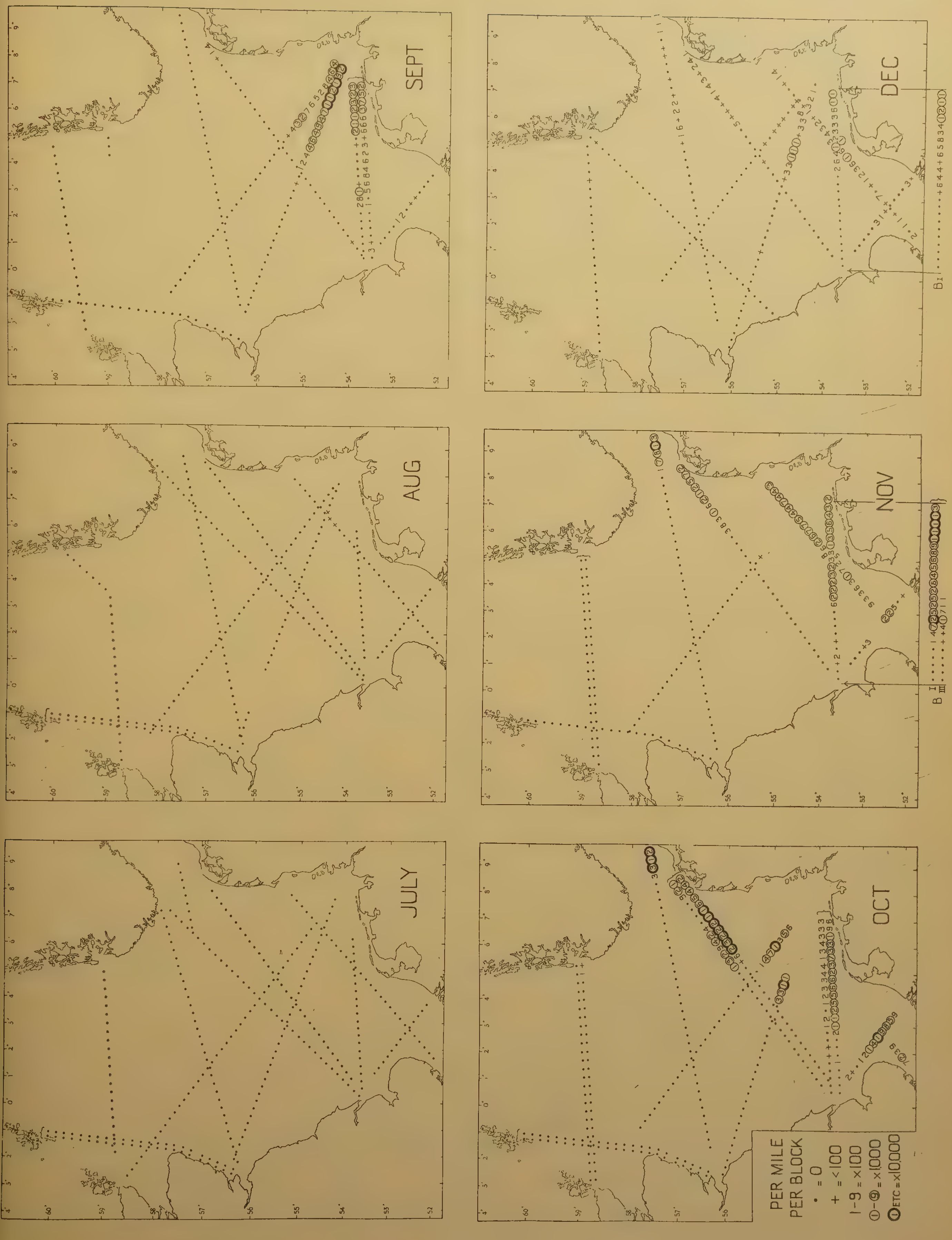

● - OCT
■ - NOV
1938

PLATE XII


MAR.
JUNE
FEB
MAY
JAN
APR

BIDDULPHIA SINENSIS
1938

PLATE XIII


JULY
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SEPT
OCT
NOV
DEC
B I
B III
B1
PER MILE
PER BLOCK
• = 0
+ = <100
1-9 = ×100
①-⑨ = ×1000
❶ETC = ×10,000

PLATE XIV

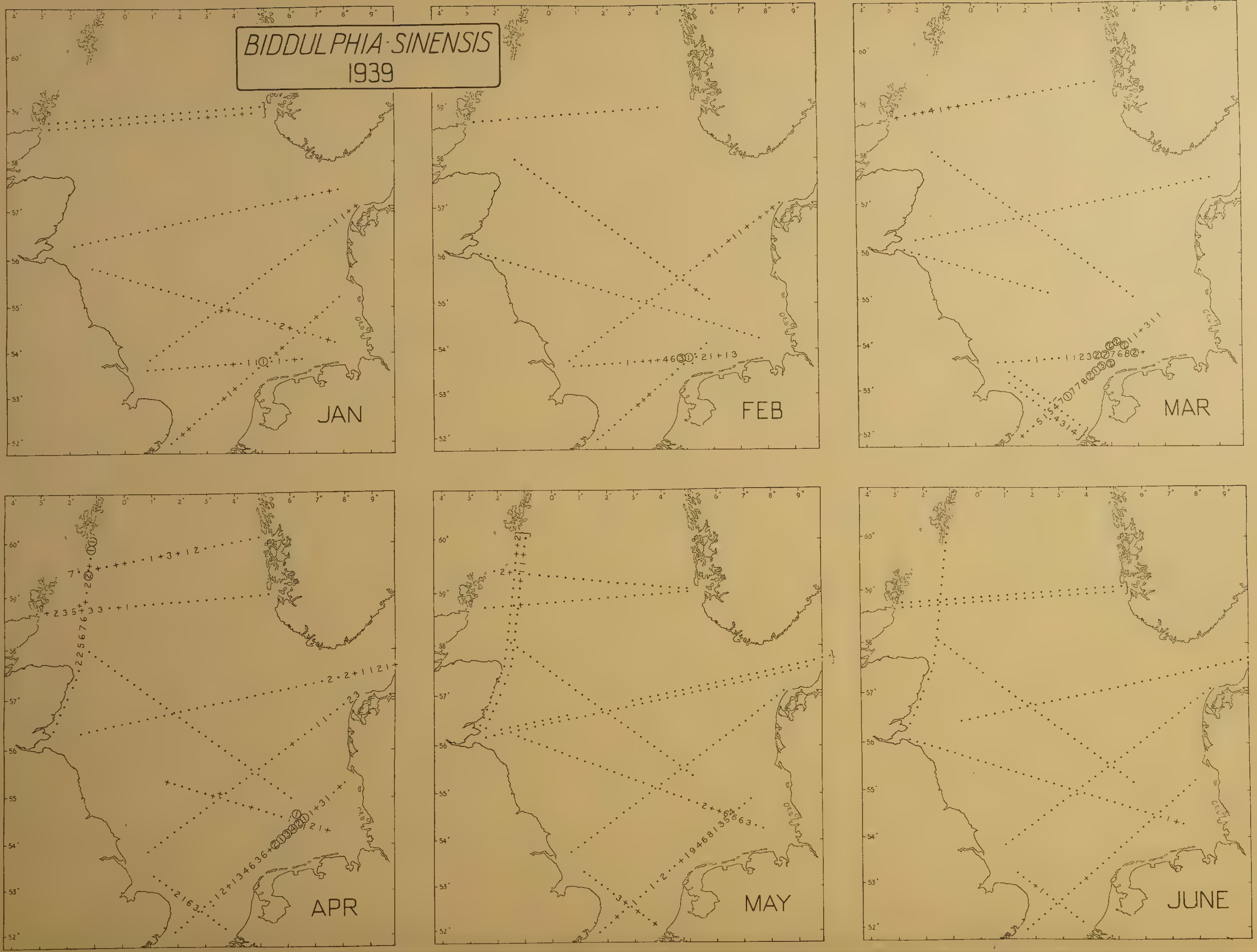
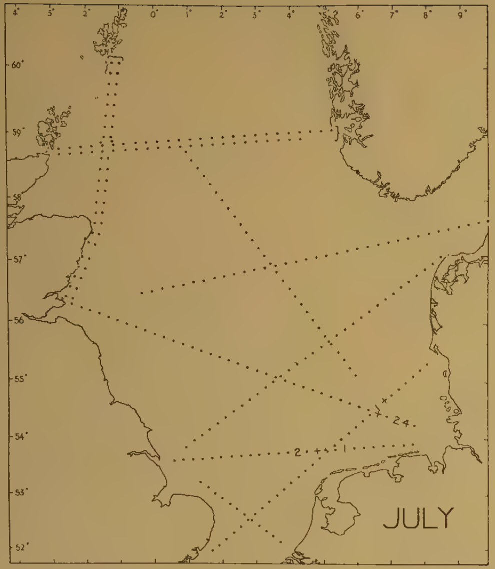
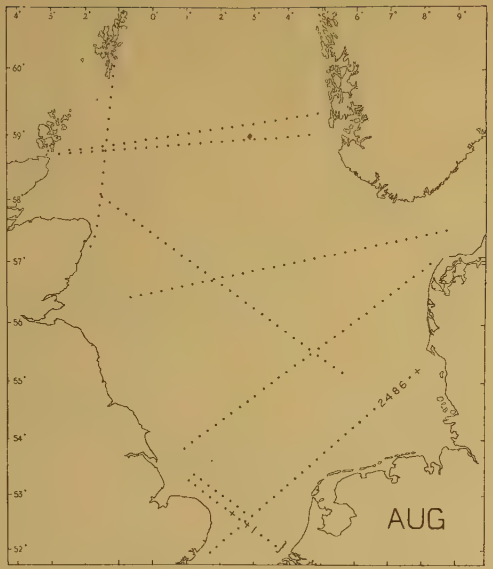

BIDDULPHIA·SINENSIS
1939
JAN
FEB
MAR
APR
MAY
JUNE

PLATE XV

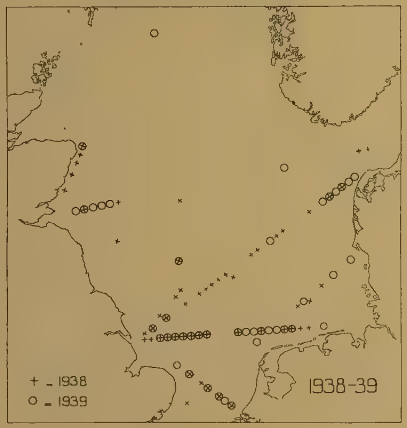
BIDDULPHIA SINENSIS
1939 CONTD.


JULY
4° 3° 2° 1° 0° 1° 2° 3° 4° 5° 6° 7° 8° 9°
60° 59° 58° 57° 56° 55° 54° 53° 52°
24
2
1

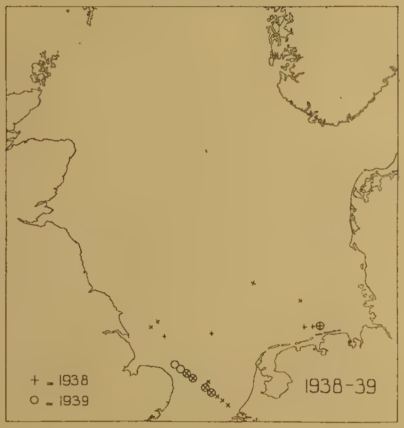

AUG
4° 3° 2° 1° 0° 1° 2° 3° 4° 5° 6° 7° 8° 9°
60° 59° 58° 57° 56° 55° 54° 53° 52°
2486
1

Single maps
showing the overall
distribution of four
other species.

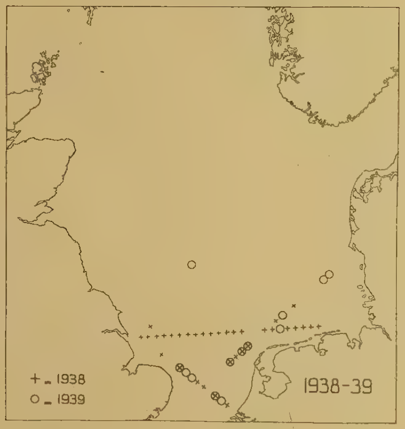
B.MOBILIENSIS


+ – 1938
o – 1939
1938-39

B. RHOMBUS


+ – 1938
o – 1939
1938-39

BELLAROCHIA


+ – 1938
o – 1939
1938-39

CORETHRON

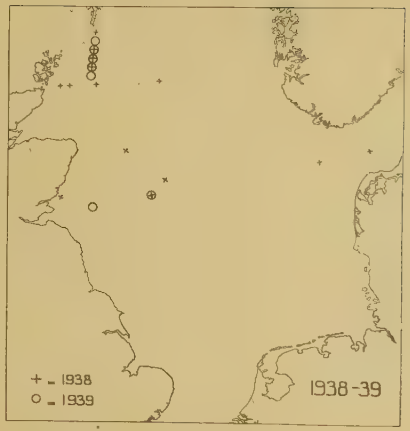
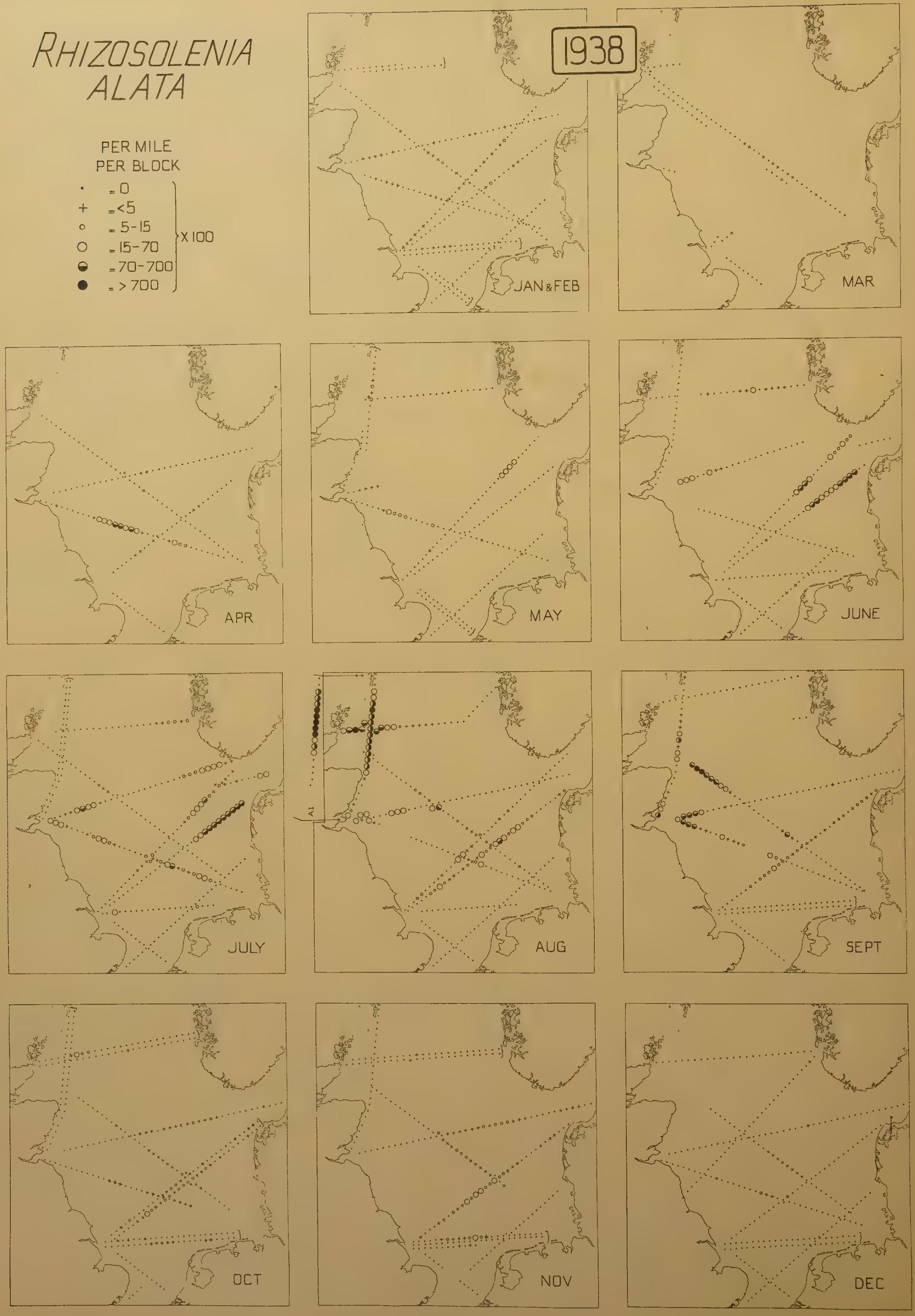
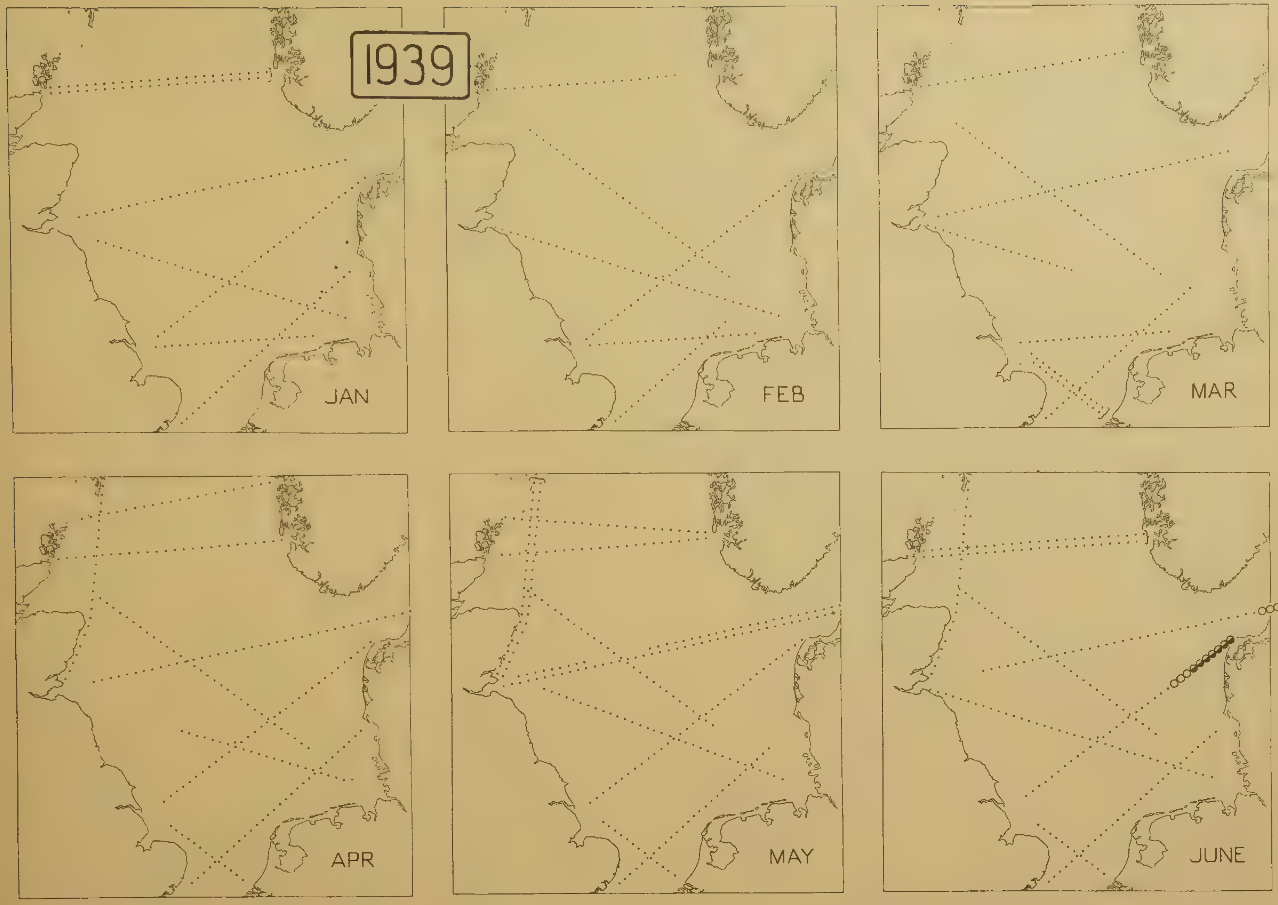
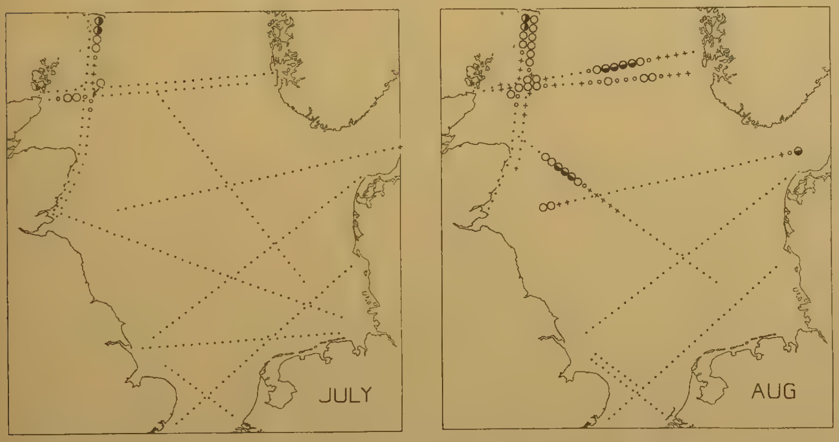

+ – 1938
o – 1939
1938-39

PLATE XVI

RHIZOSOLENIA ALATA


PER MILE
PER BLOCK
· = 0
+ = <5
∘ = 5-15
○ = 15-70
◒ = 70-700
● = >700
X 100
1938
JAN & FEB
MAR
APR
MAY
JUNE
JULY
A1
AUG
SEPT
OCT
NOV
DEC


1939
JAN
FEB
MAR
APR
MAY
JUNE



BIDDULPHIA REGIA

showing two maps of the larger patches [scale as above] and the overall distribution 1938-9.

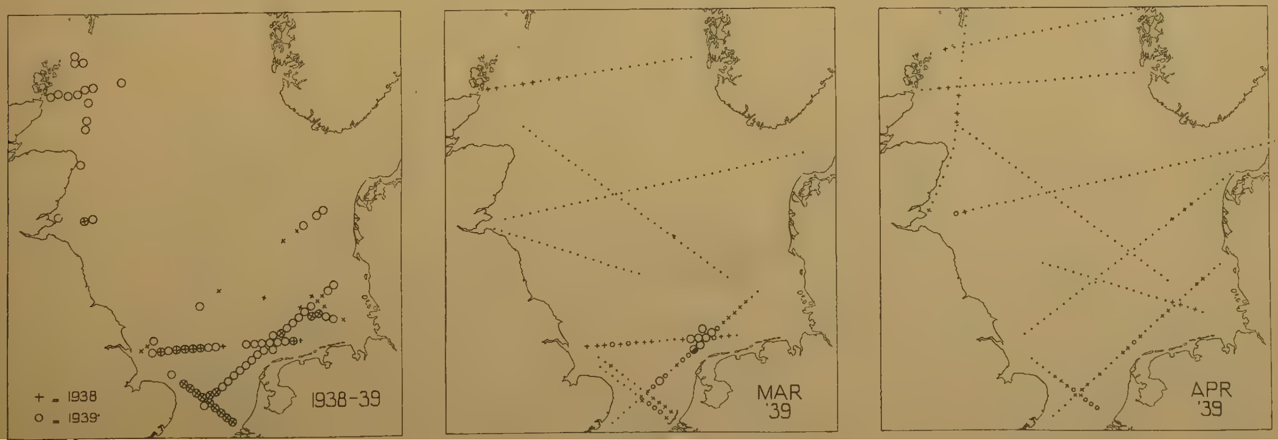
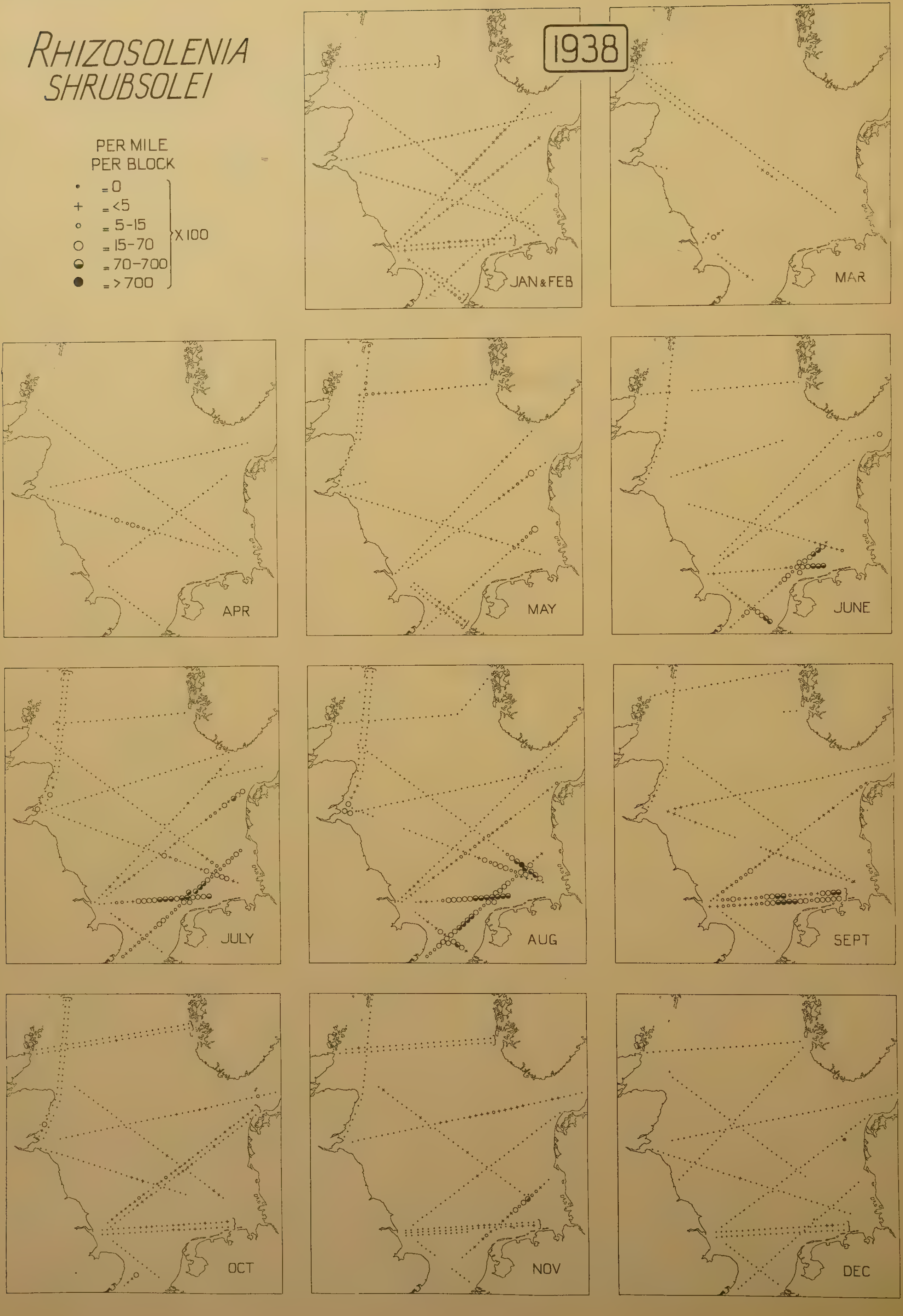

+ = 1938
o = 1939
1938-39
MAR '39
APR '39

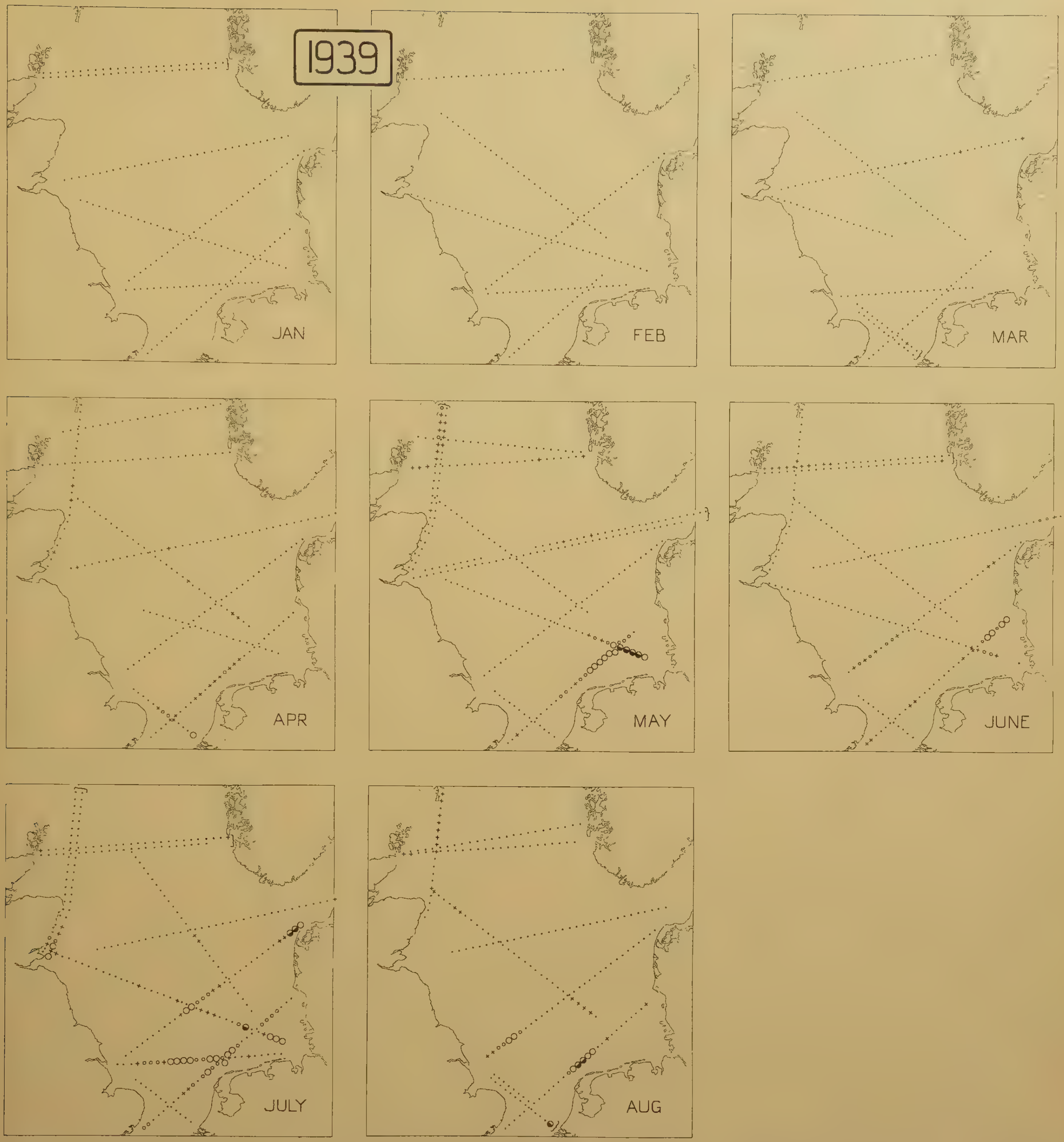
PLATE XVIII

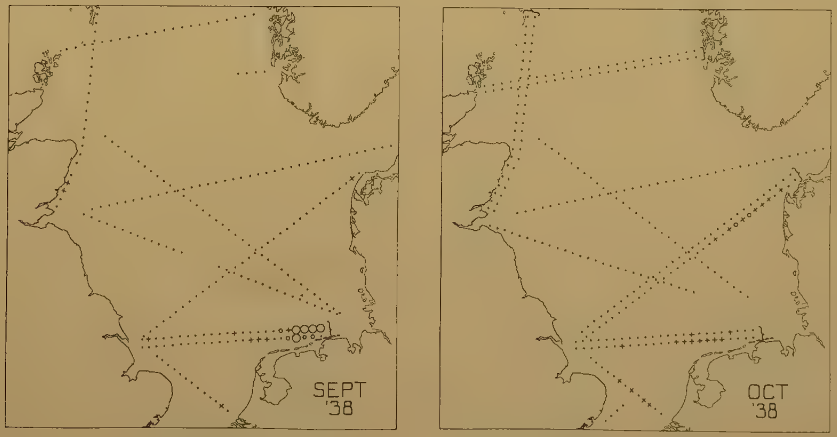
RHIZOSOLENIA SHRUBSOLEI

PER MILE
PER BLOCK
· = 0
+ = <5
∘ = 5-15
○ = 15-70
◒ = 70-700
● = >700
} X 100



1938
JAN & FEB
MAR
APR
MAY
JUNE
JULY
AUG
SEPT
OCT
NOV
DEC


1939
JAN
FEB
MAR
APR
MAY
JUNE
JULY
AUG


SEPT
'38
OCT
'38

BIDDULPHIA ALTERNANS showing maps of the larger patches.

PLATE XX

RHIZOSOLENIA SEMISPINA

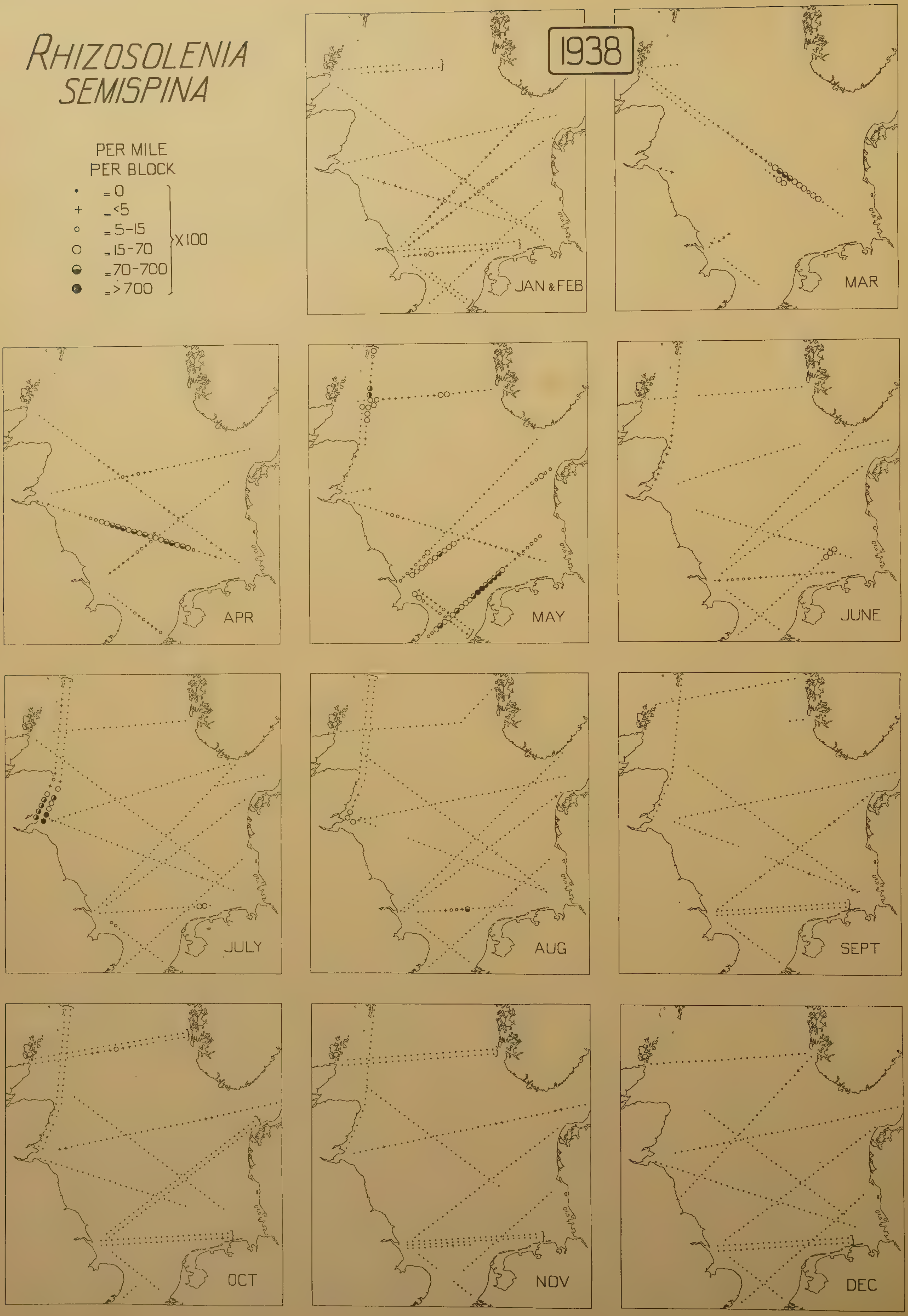
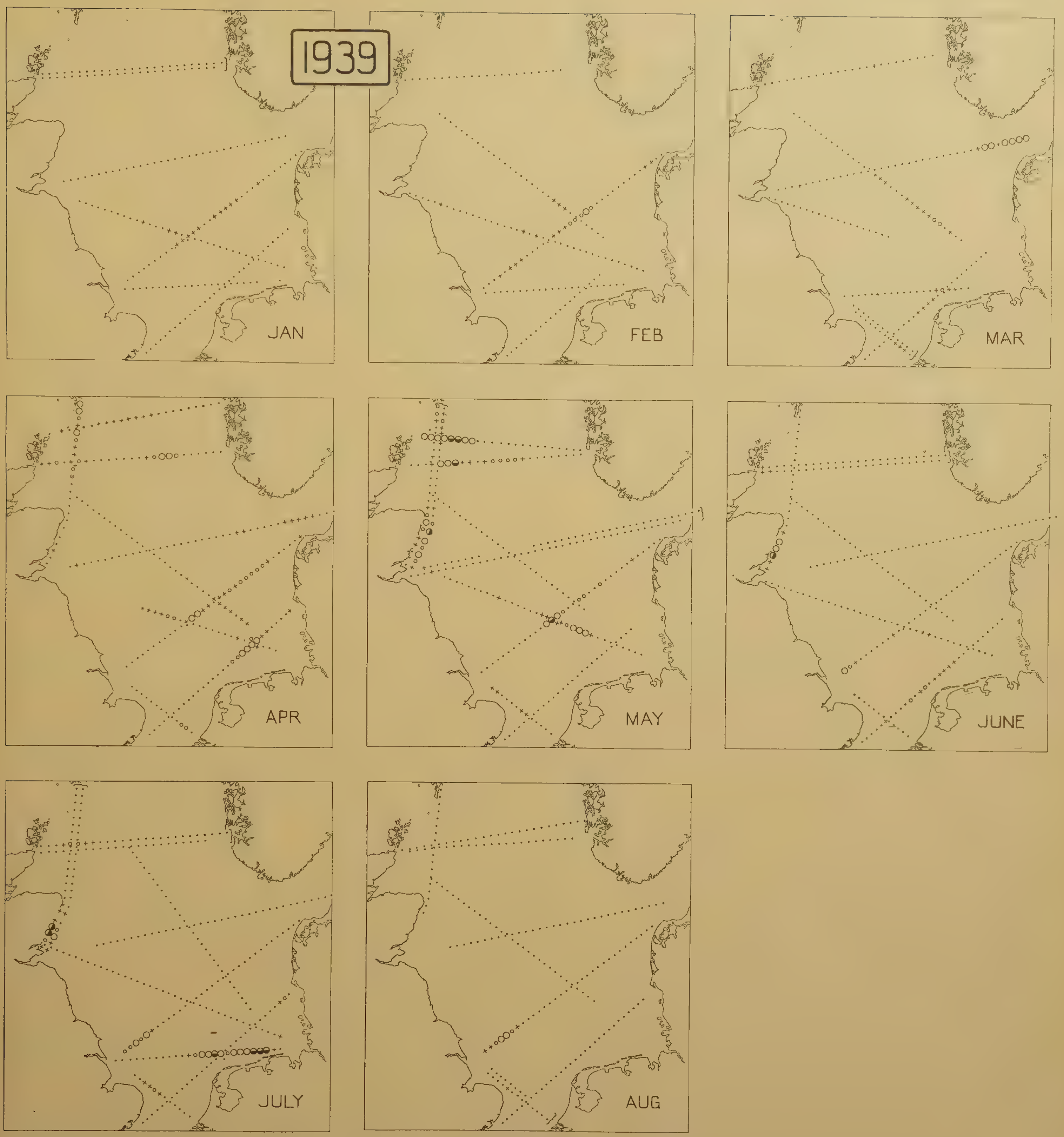

PER MILE
PER BLOCK
• = 0
+ = <5
○ = 5-15
◯ = 15-70
◒ = 70-700
● = >700
X100
1938
JAN & FEB
MAR
APR
MAY
JUNE
JULY
AUG
SEPT
OCT
NOV
DEC

PLATE XXI


1939
JAN
FEB
MAR
APR
MAY
JUNE
JULY
AUG

CERATAULINA BERGONII
showing maps
of the larger patches
of 1939

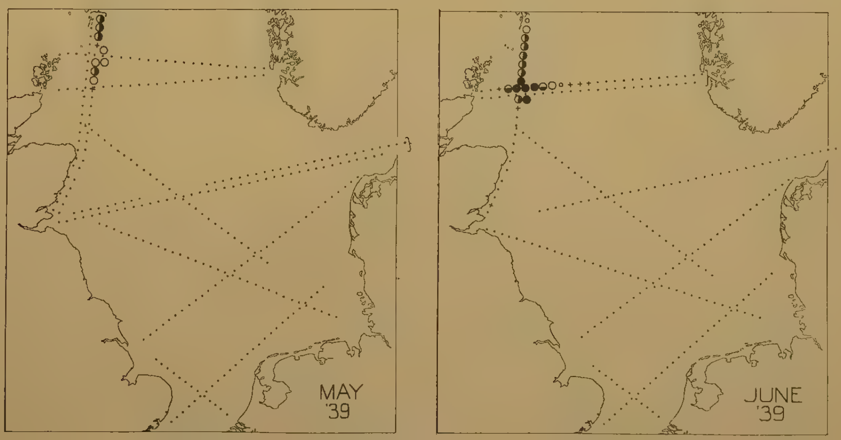

MAY '39
JUNE '39

PLATE XXII

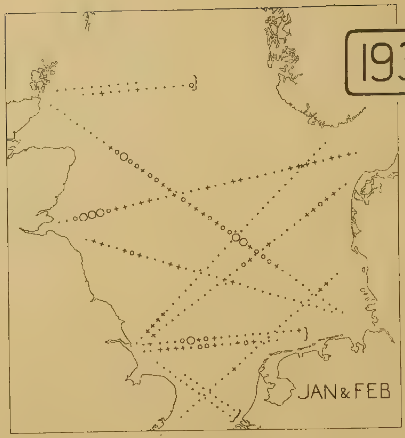
THALASSIOSIRA*
[SPP.]

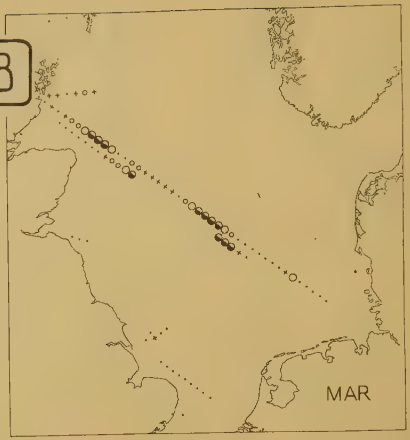
PER MILE
PER BLOCK

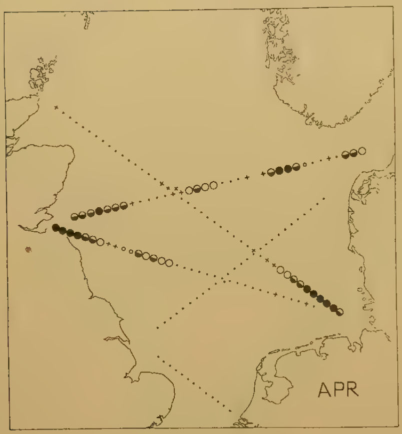
·	= 0
+	= <5
∘	= 5–15
○	= 15–70
◒	= 70–700
●	= > 700

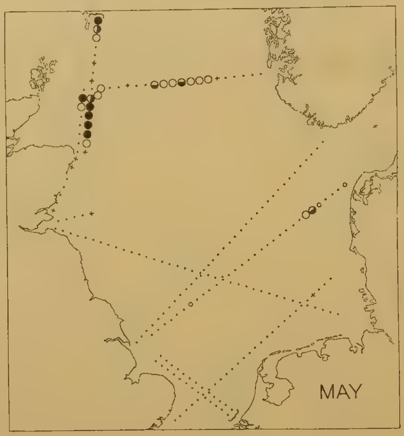
} X 100

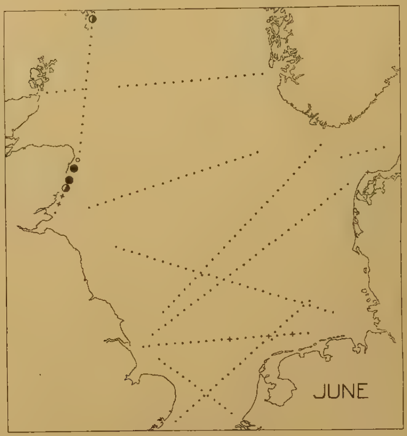
1938

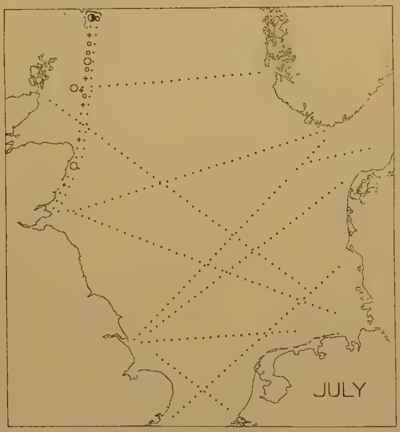


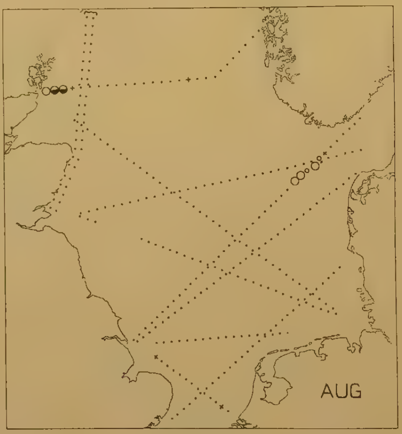


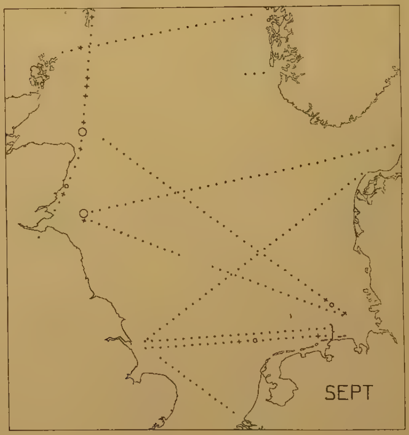


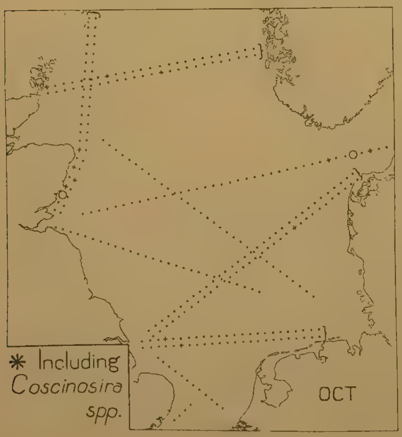


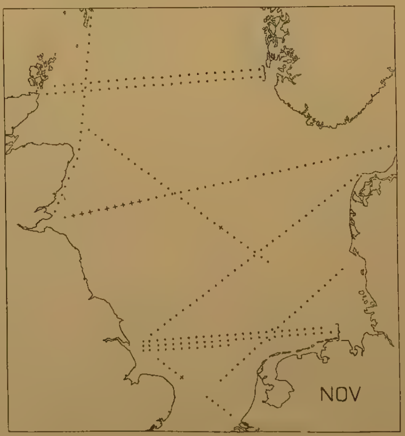


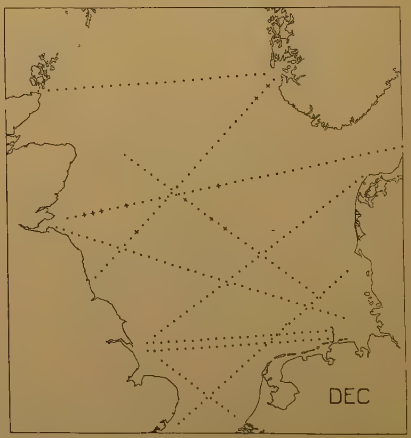








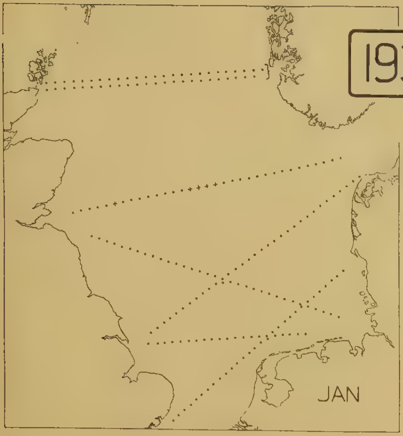


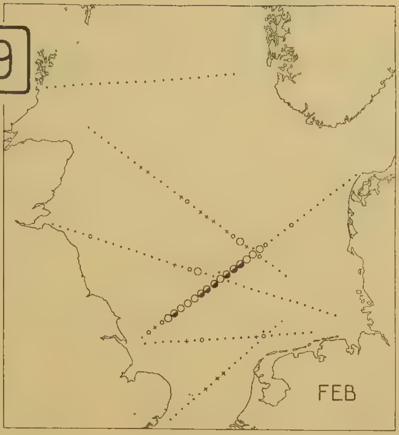


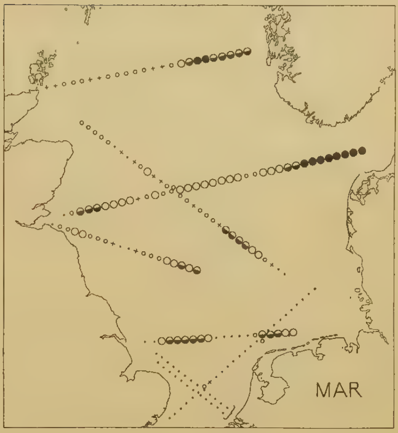
* Including *Coscinosira* spp.

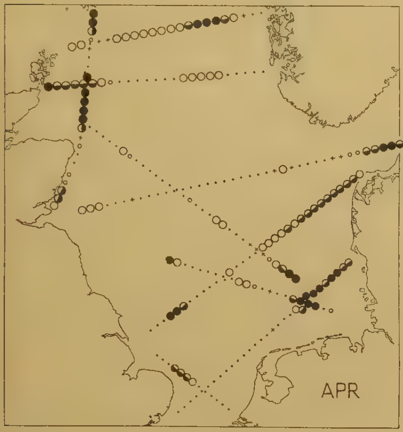
PLATE XXIII

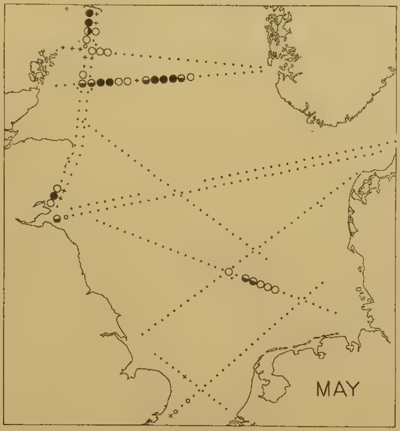
1939

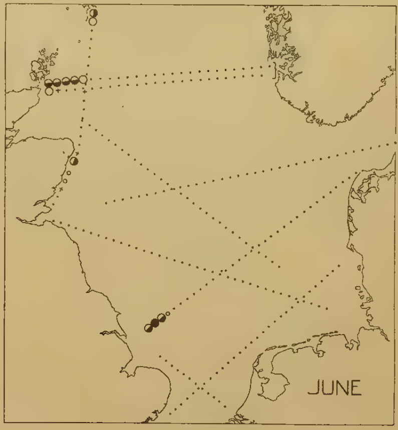


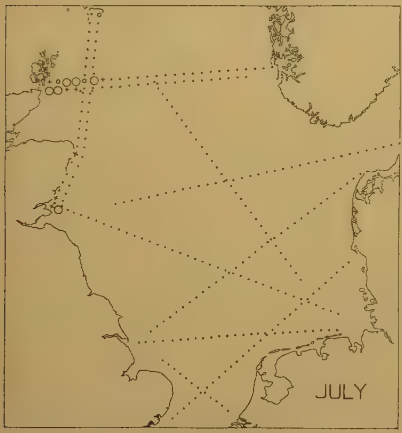


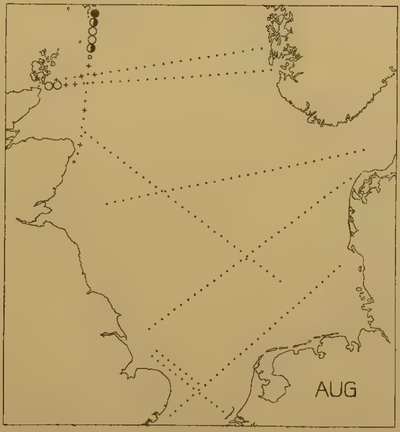




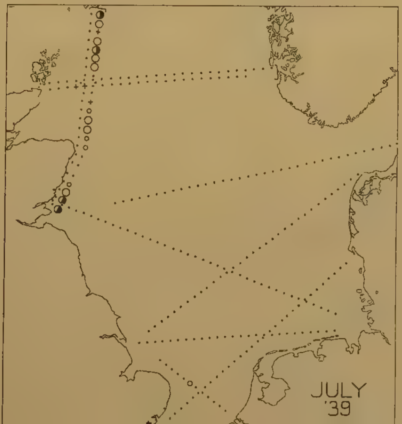








RHIZOSOLENIA FAEROENSE
showing maps of
the larger patches
of 1939



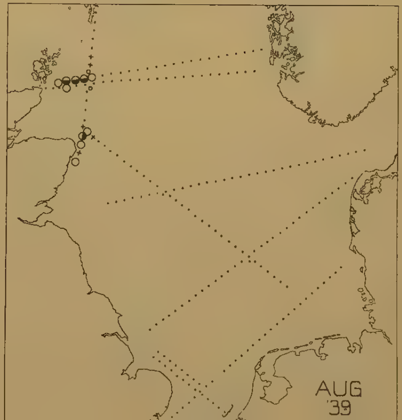


PLATE XXIV

CHAETOCEROS [PHAEOCERIDS]

PER MILE
PER BLOCK

· = 0
+ = <5
∘ = 5–15
○ = 15–70
◒ = 70–700
● = >700
}X100

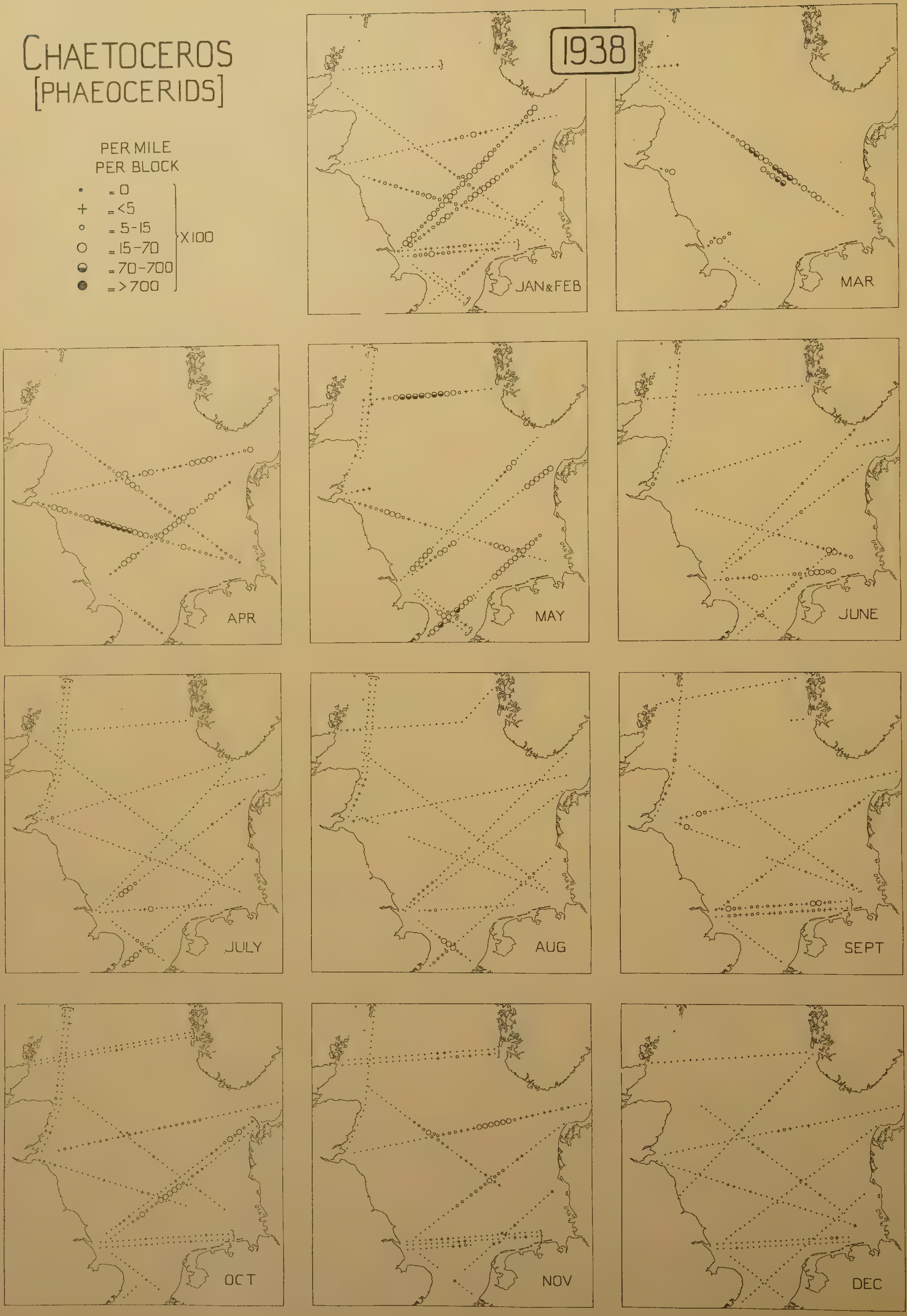
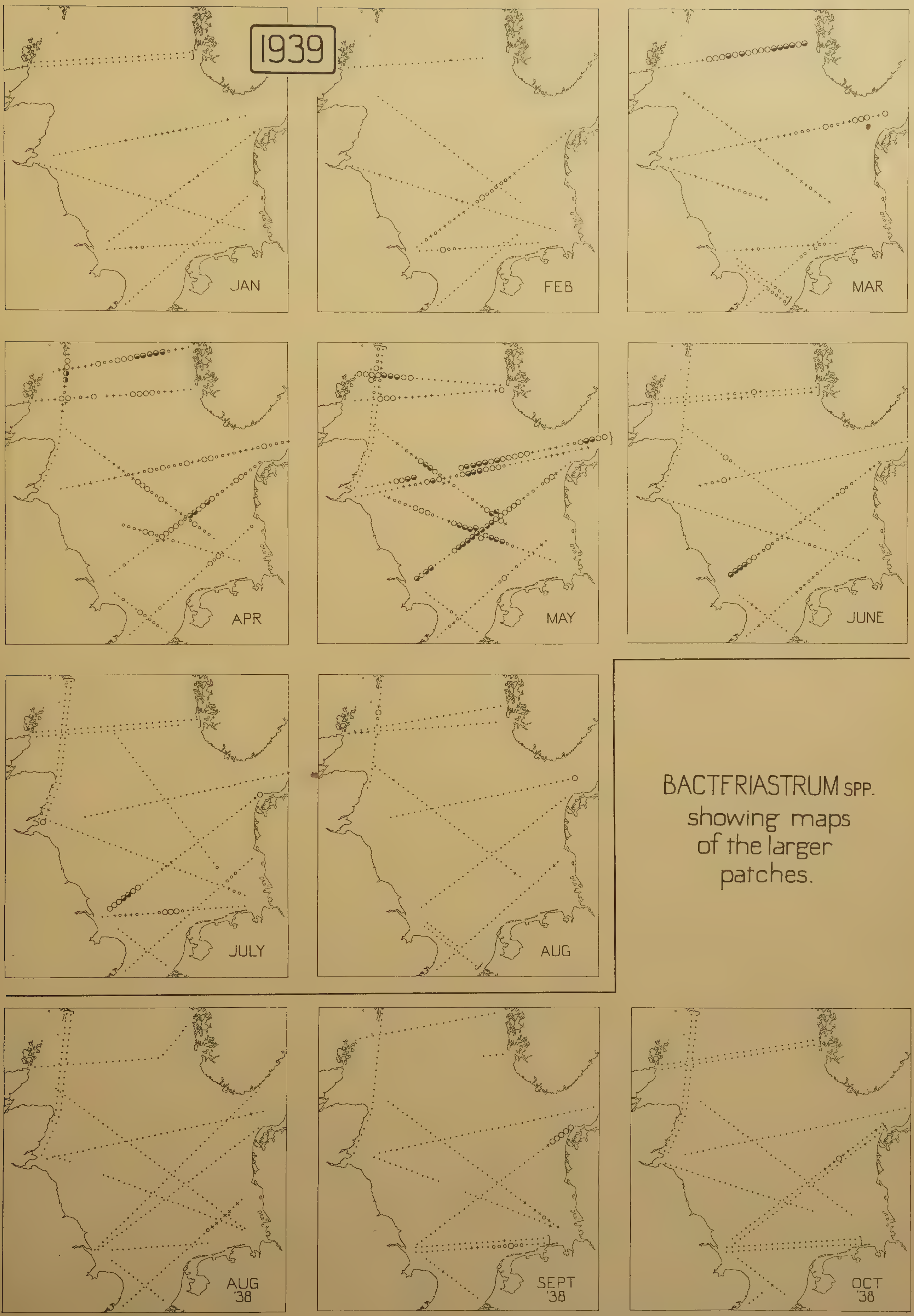

1938
JAN & FEB
MAR
APR
MAY
JUNE
JULY
AUG
SEPT
OCT
NOV
DEC

PLATE XXV


1939
JAN
FEB
MAR
APR
MAY
JUNE
JULY
AUG
AUG '38
SEPT '38
OCT '38

BACTERIASTRUM SPP.
showing maps
of the larger
patches.

PLATE XXVI

CHAETOCEROS DECIPIENS

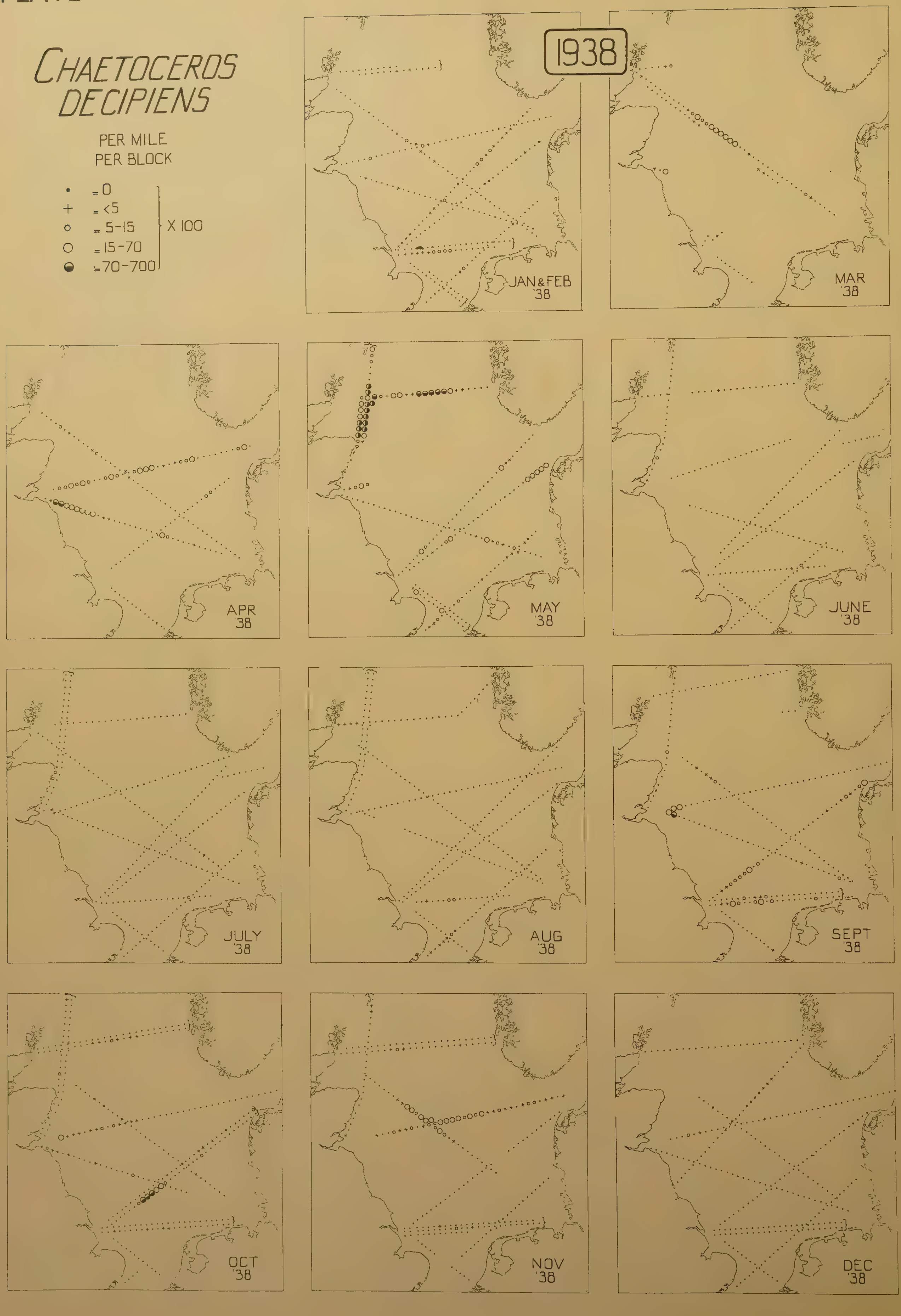
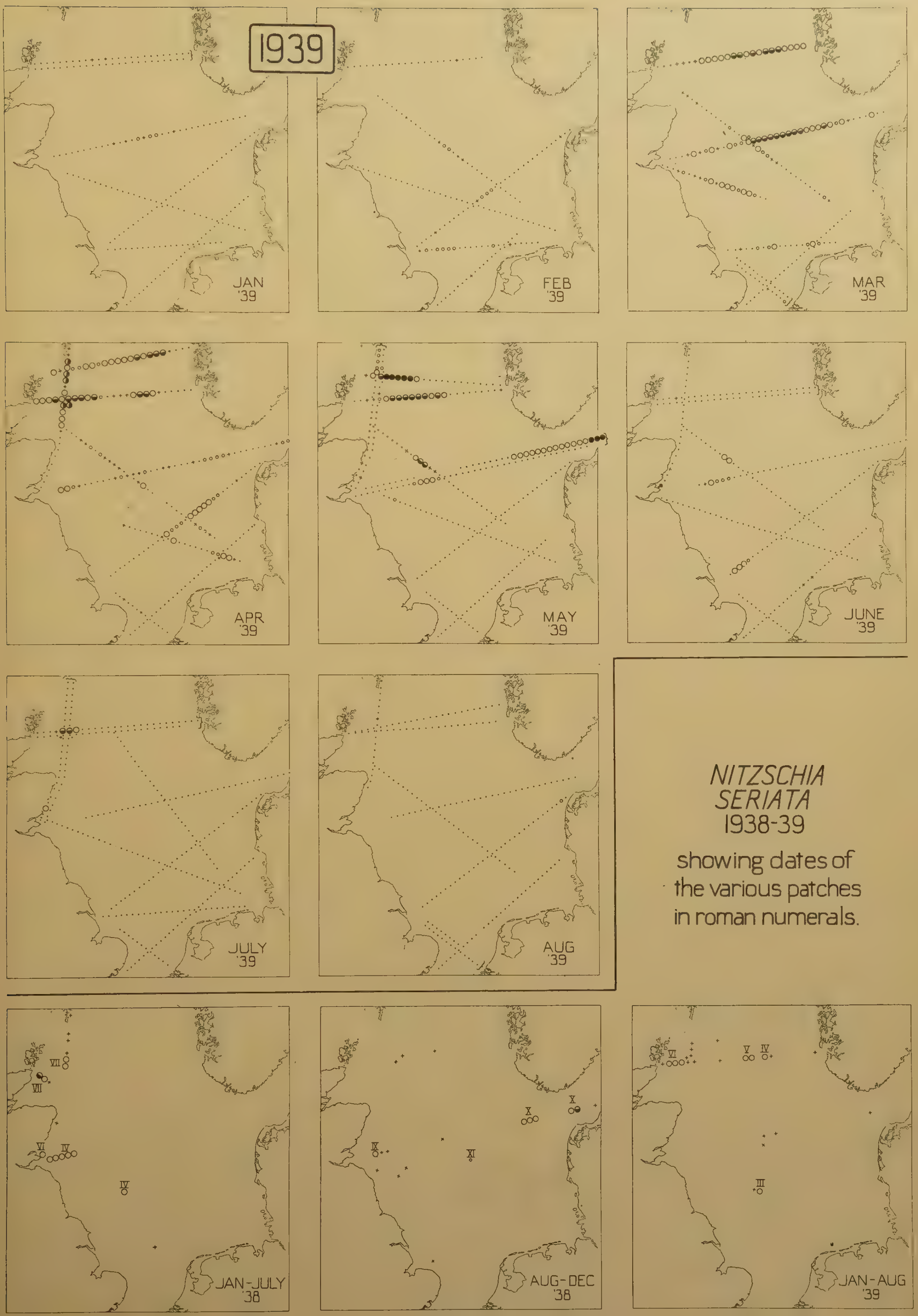

PER MILE
PER BLOCK
• = 0
+ = <5
∘ = 5-15
○ = 15-70
◒ = 70-700
X 100
1938
JAN & FEB '38
MAR '38
APR '38
MAY '38
JUNE '38
JULY '38
AUG '38
SEPT '38
OCT '38
NOV '38
DEC '38

PLATE XXVII

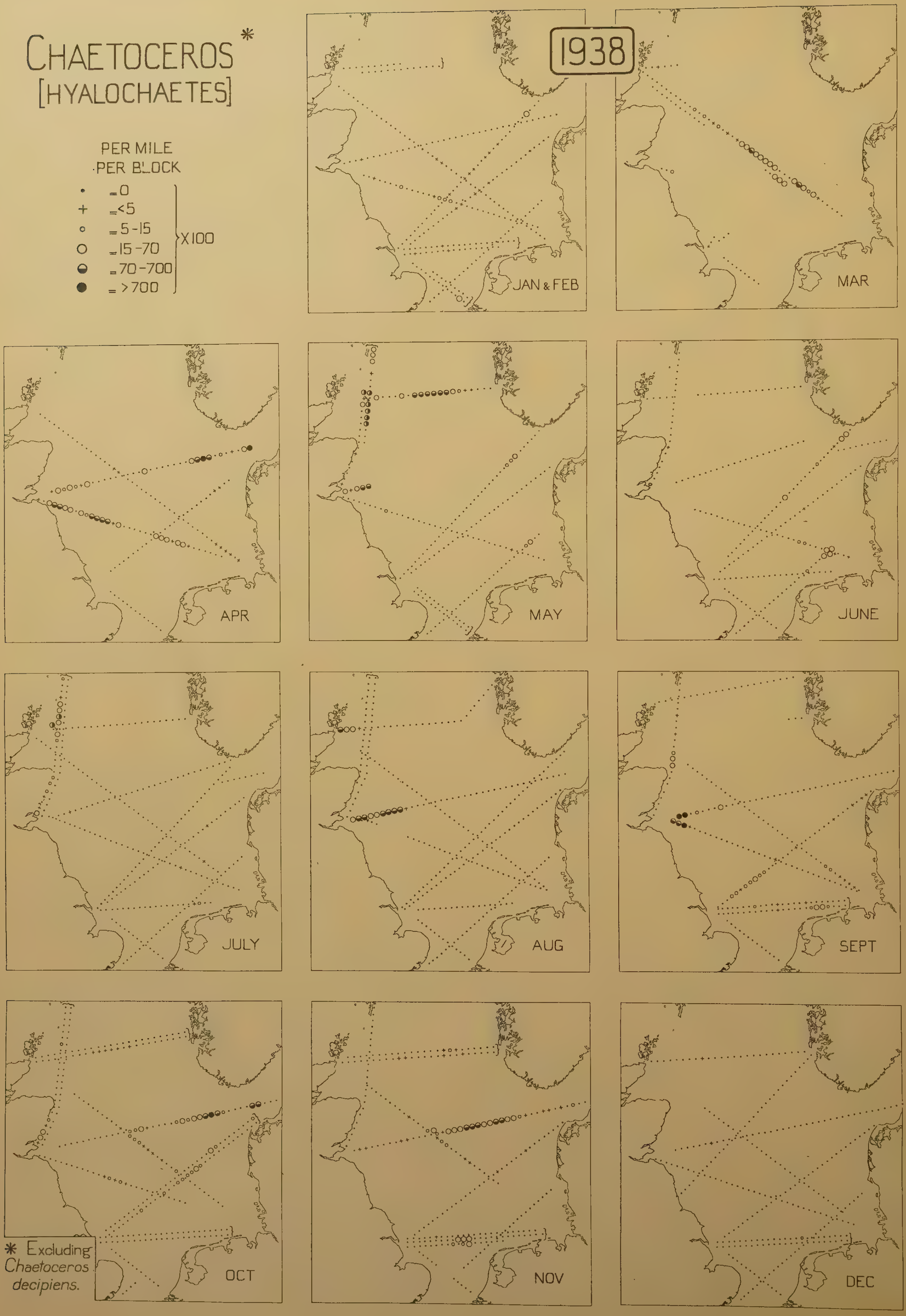

1939
JAN '39
FEB '39
MAR '39
APR '39
MAY '39
JUNE '39
JULY '39
AUG '39
VII
VIII
VI
IV
IV
JAN-JULY '38
IX
X
X
XI
AUG-DEC '38
VI
V
IV
III
JAN-AUG '39

NITZSCHIA SERIATA
1938-39

showing dates of the various patches in roman numerals.

PLATE XXVIII

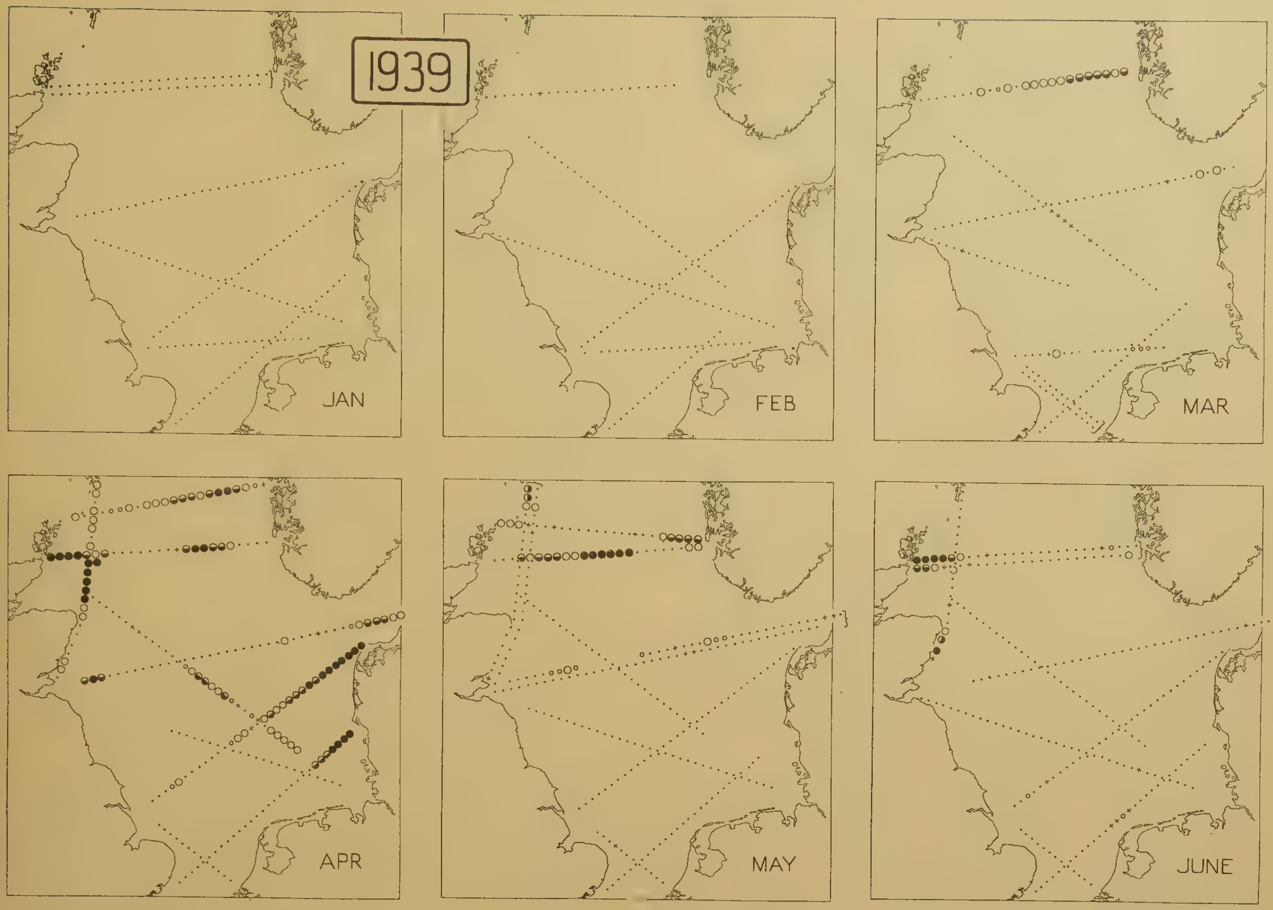
CHAETOCEROS*
[HYALOCHAETES]

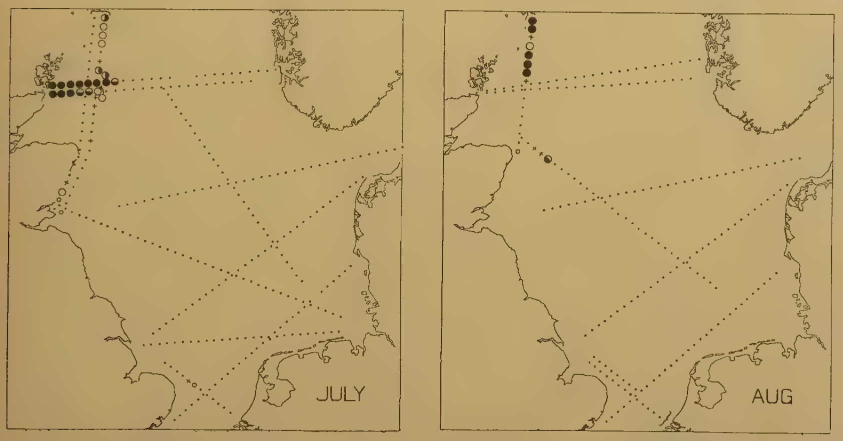

1938
JAN & FEB
MAR
APR
MAY
JUNE
JULY
AUG
SEPT
OCT
NOV
DEC

PER MILE
PER BLOCK

•	= 0	X100
+	= <5	
∘	= 5-15	
○	= 15-70	
◐	= 70-700	
●	= >700	

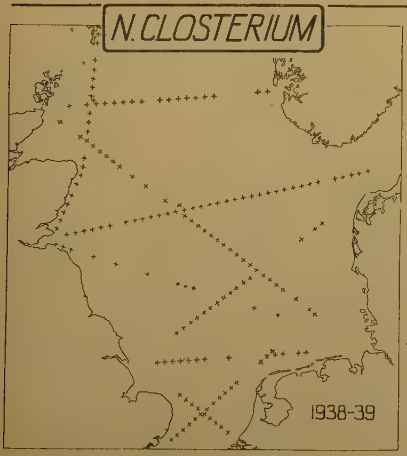
* Excluding *Chaetoceros decipiens.*


1939
JAN
FEB
MAR
APR
MAY
JUNE

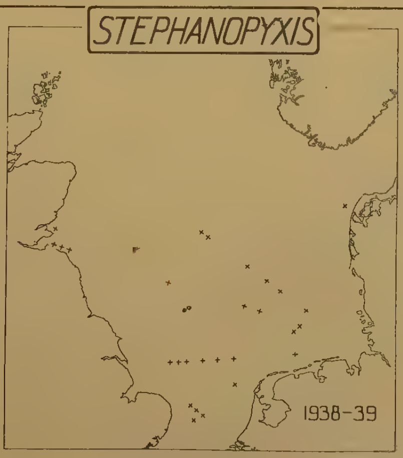


Single maps showing the overall distributions of three other diatoms.

N. CLOSTERIUM



STEPHANOPYXIS



GUINARDIA

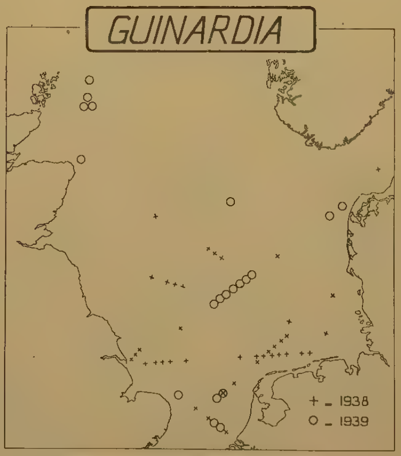
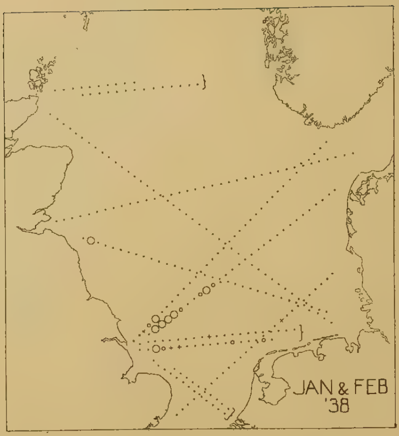


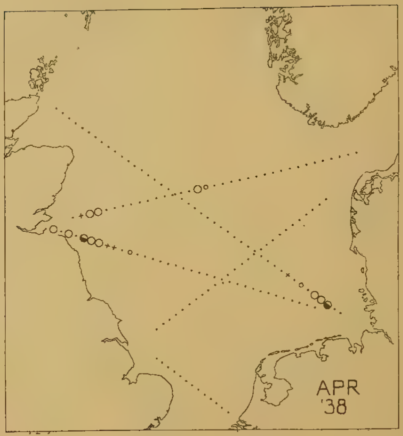
PLATE XXX

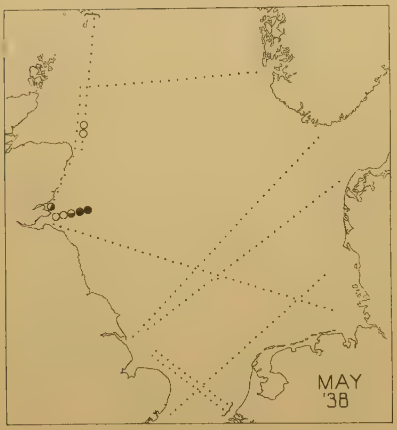
ASTERIONELLA JAPONICA

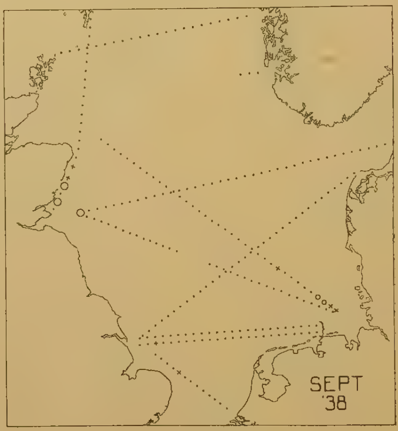
PER MILE
PER BLOCK

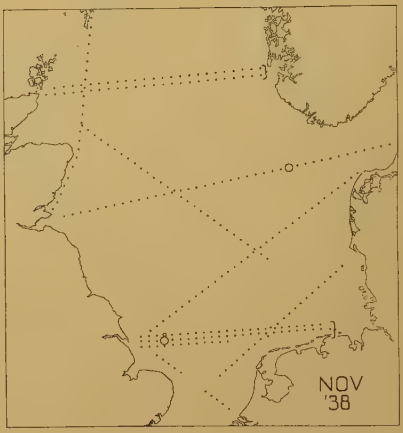
• = 0
+ = <5
∘ = 5-15
○ = 15-70
◒ = 70-700
● = >700
} X 100

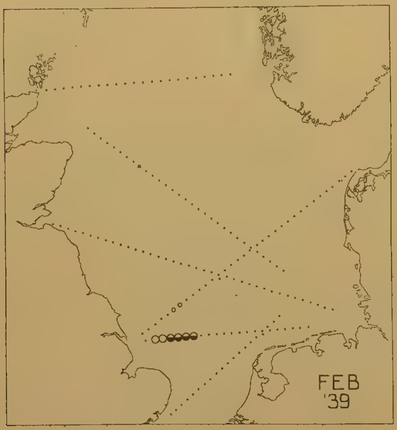


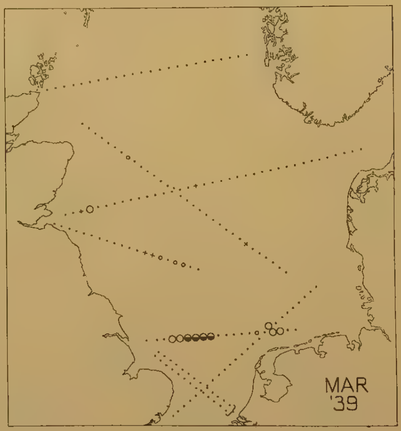


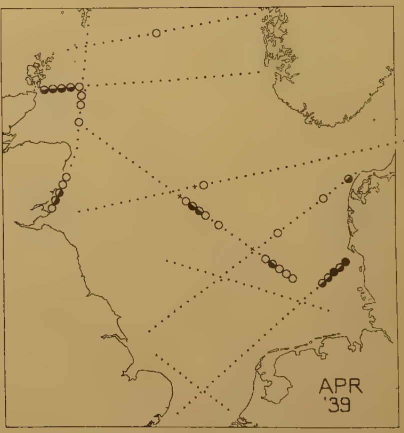


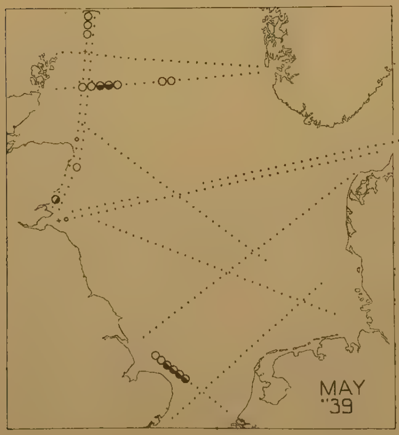


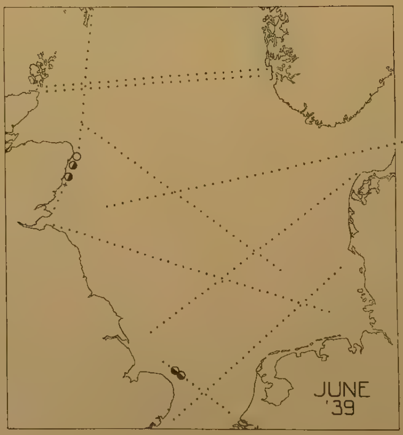


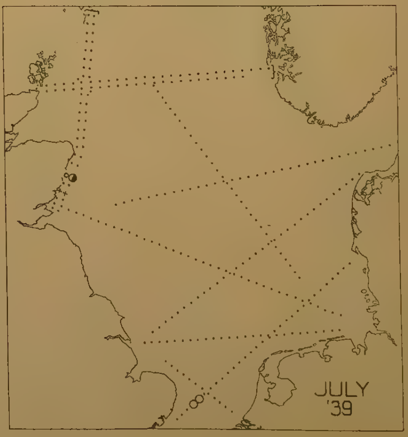


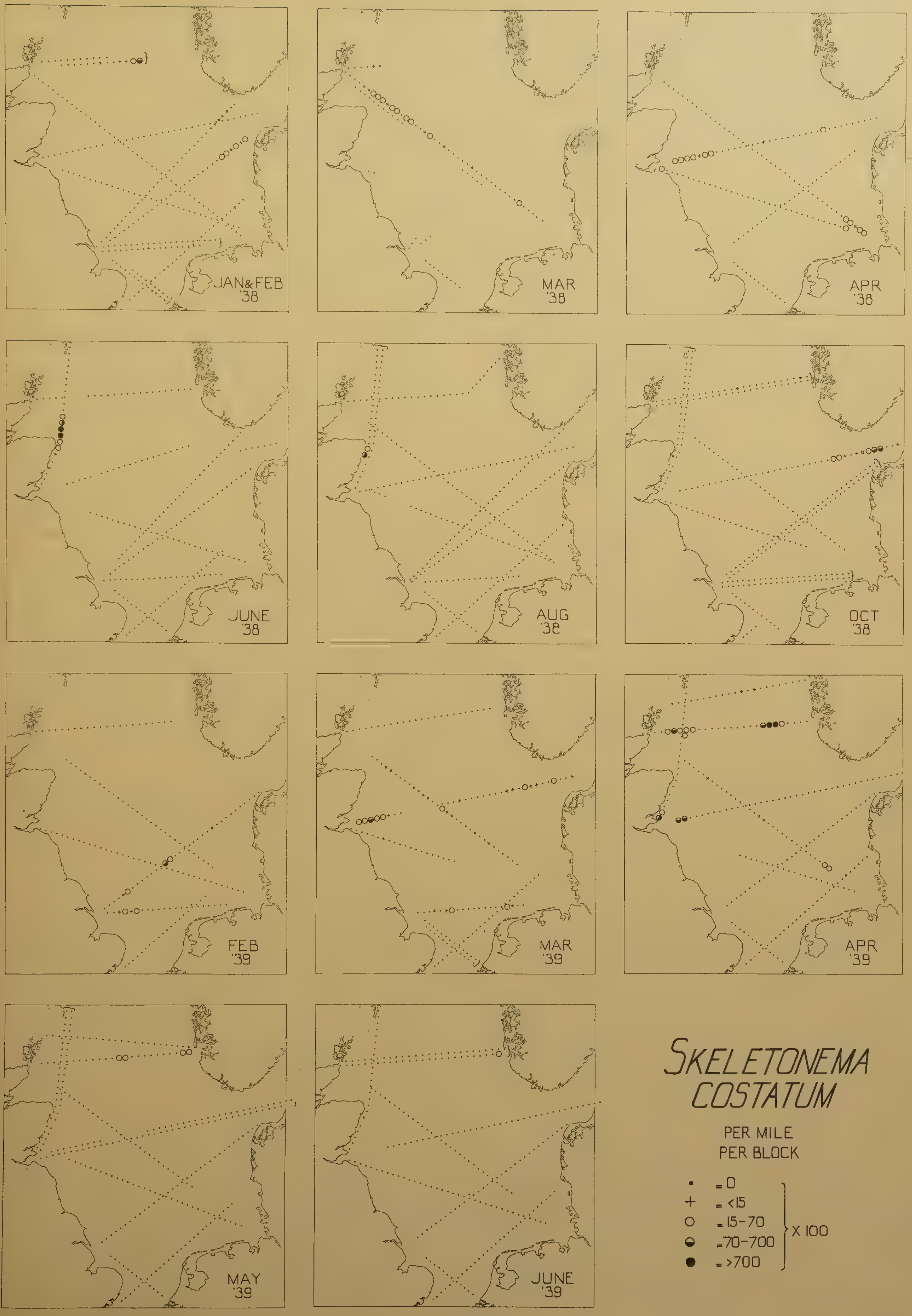











JAN&FEB '38
MAR '38
APR '38
JUNE '38
AUG '38
OCT '38
FEB '39
MAR '39
APR '39
MAY '39
JUNE '39

SKELETONEMA COSTATUM

PER MILE
PER BLOCK

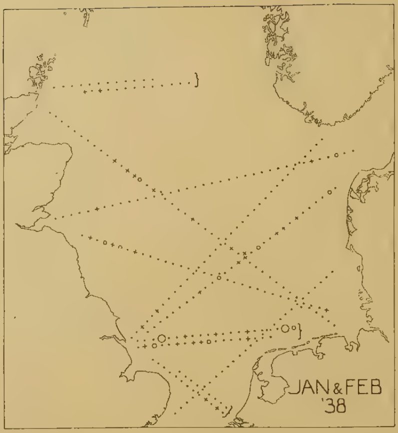
• = 0
+ = <15
○ = 15-70
◒ = 70-700
● = >700
} X 100

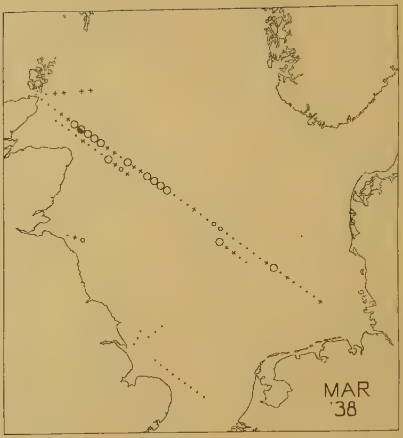
PLATE XXXII

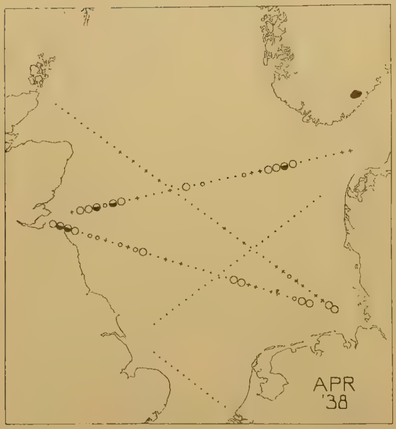
THALASSIOTHRIX NITZSCHIOIDES

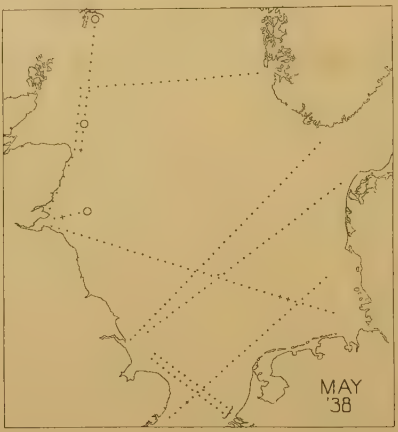
PER MILE
PER BLOCK

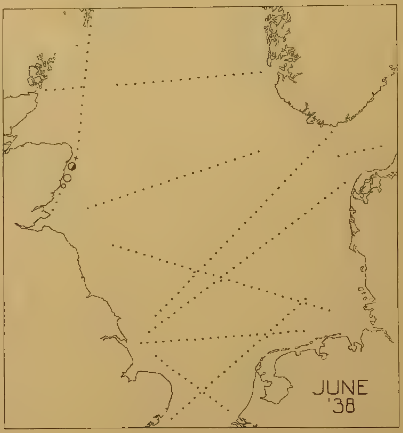
· = 0
+ = <5
∘ = 5-15
○ = 15-70
◒ = 70-700
● = >700
} X 100

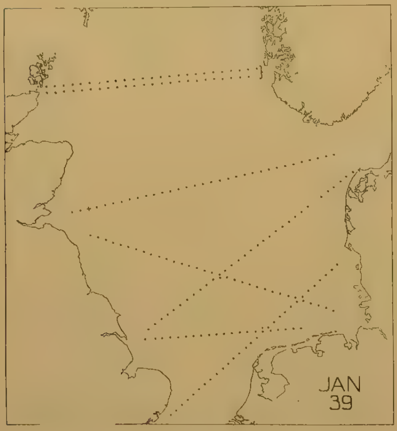


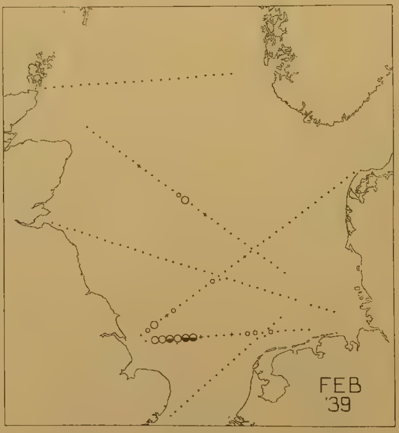


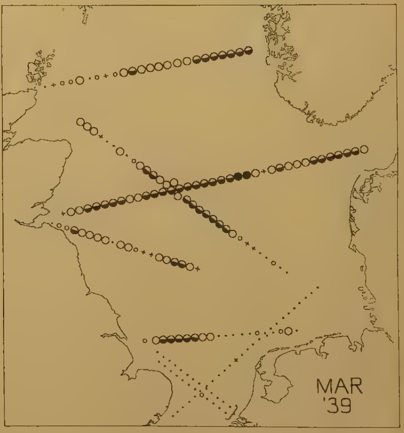


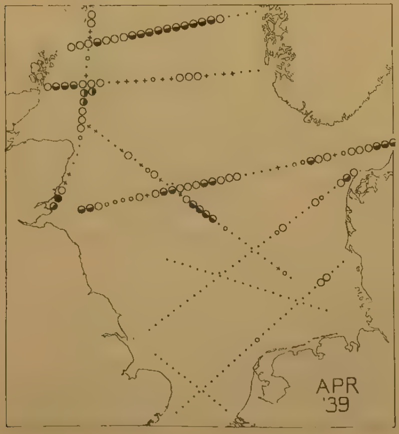


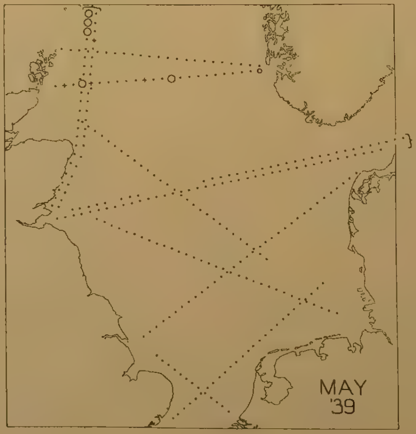


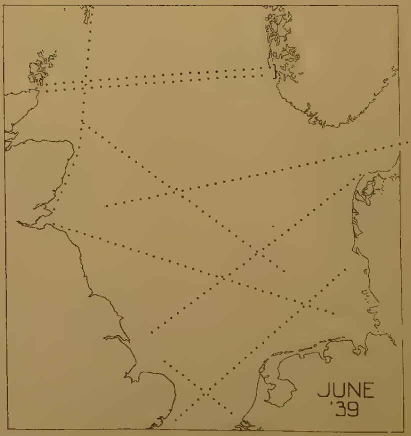


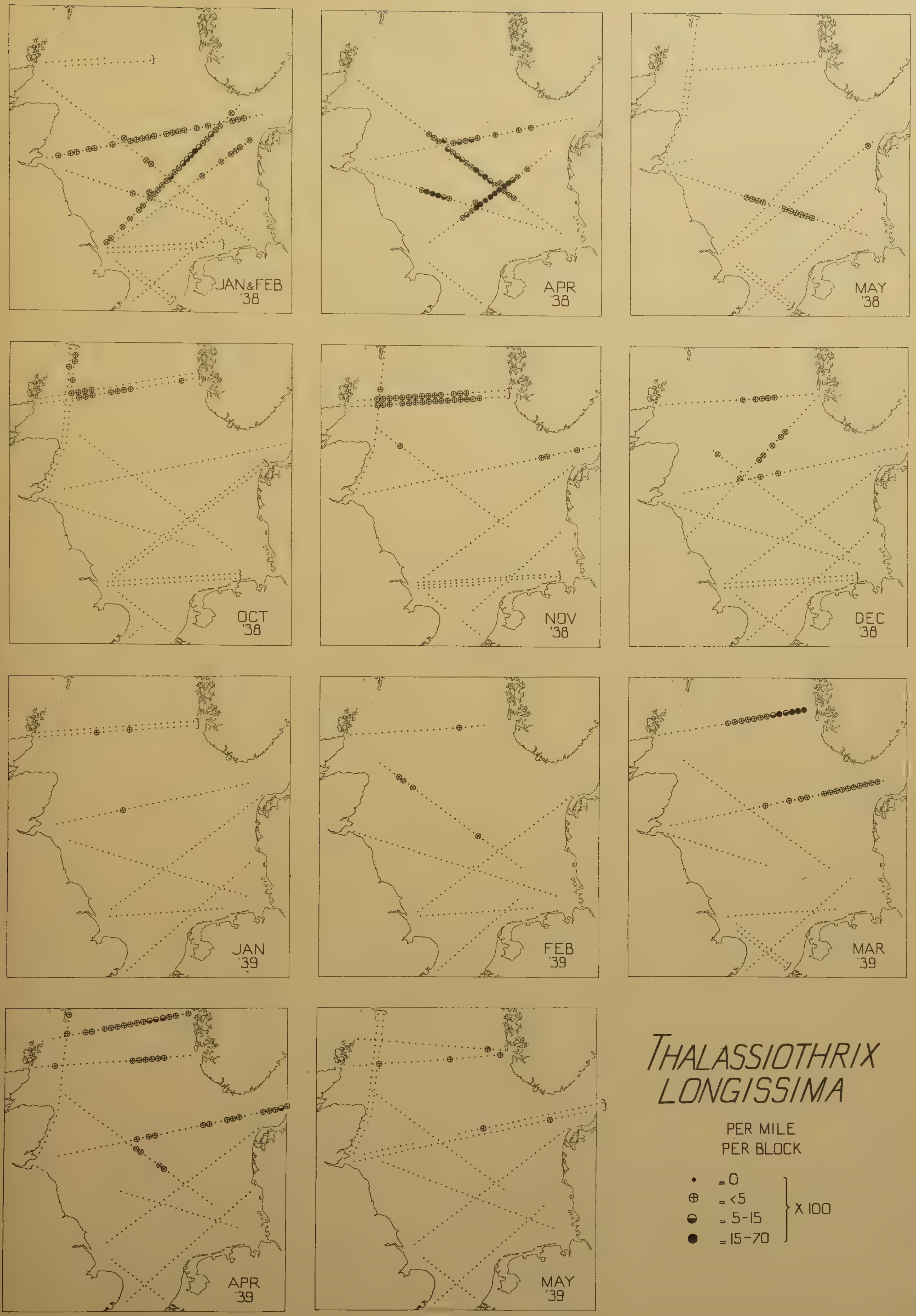











JAN & FEB '38
APR '38
MAY '38
OCT '38
NOV '38
DEC '38
JAN '39
FEB '39
MAR '39
APR '39
MAY '39
PER MILE
PER BLOCK
• = 0
⊕ = <5
◒ = 5-15
● = 15-70
X 100

THALASSIOTHRIX LONGISSIMA

PLATE XXXIV

RHIZOSOLENIA STOLTERFOTHII

PER MILE
PER BLOCK

· = 0
+ = <5
○ = 5-15
◯ = 15-70
◓ = 70-700
● = >700
} X 100

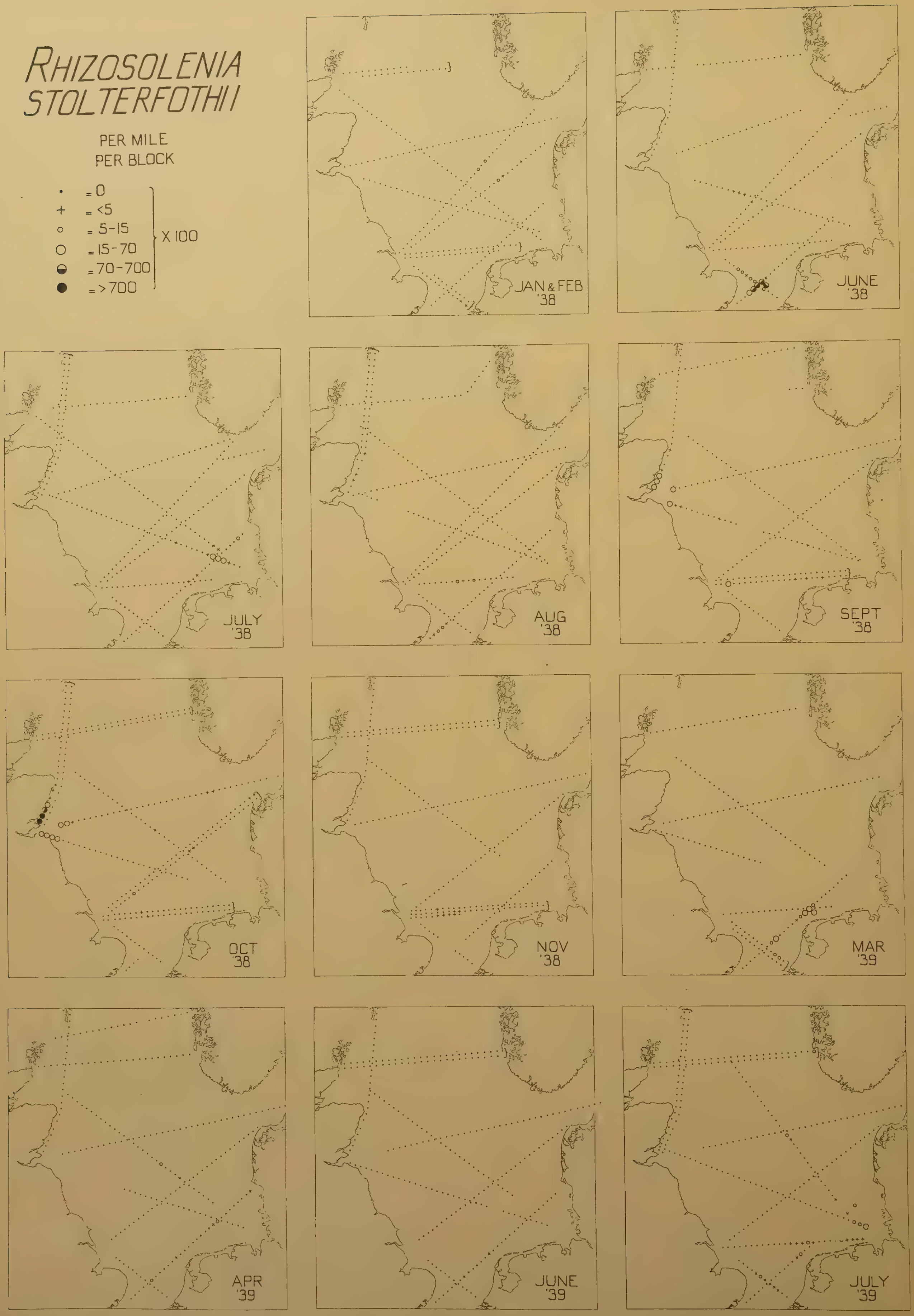
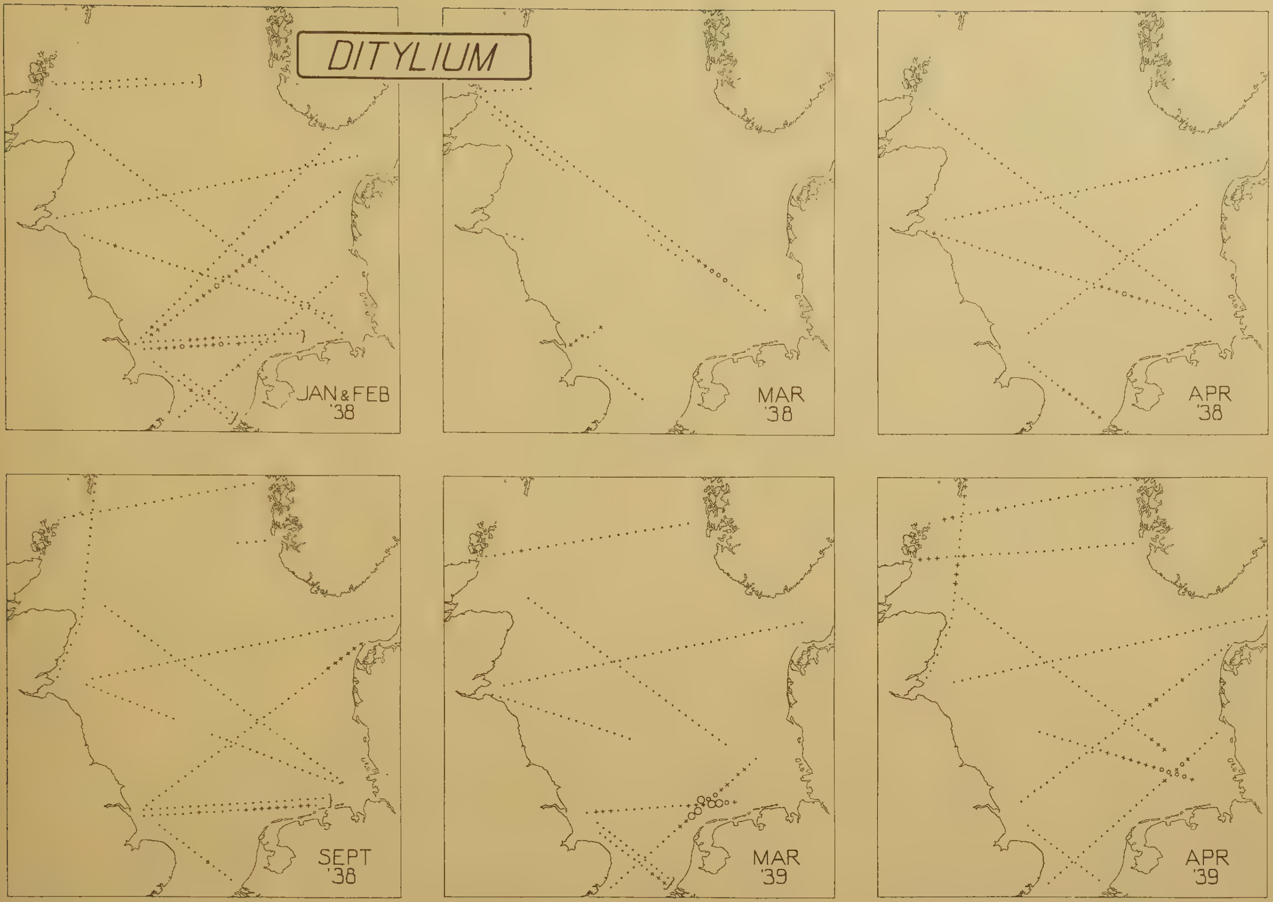

JAN & FEB '38
JUNE '38
JULY '38
AUG '38
SEPT '38
OCT '38
NOV '38
MAR '39
APR '39
JUNE '39
JULY '39

PLATE XXXV


DITYLIUM
JAN&FEB '38
MAR '38
APR '38
SEPT '38
MAR '39
APR '39

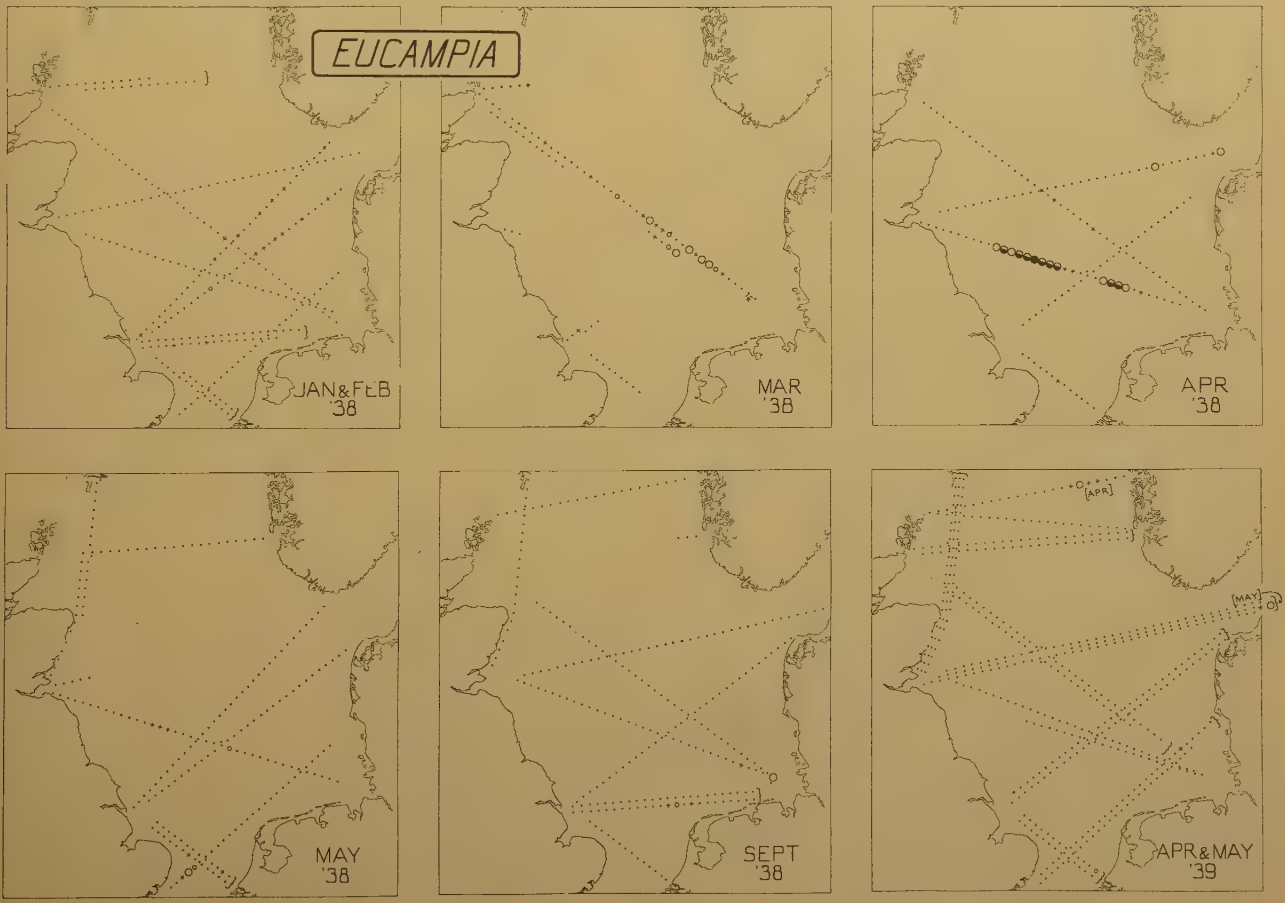
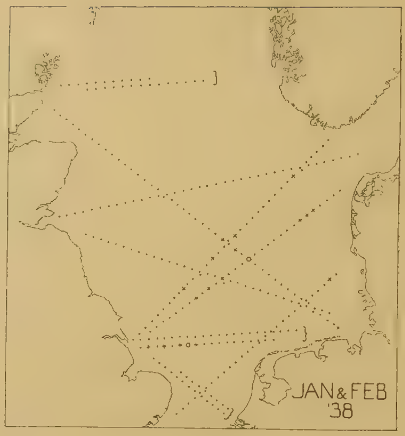

EUCAMPIA
JAN&FEB '38
MAR '38
APR '38
MAY '38
SEPT '38
[APR]
[MAY]
APR&MAY '39

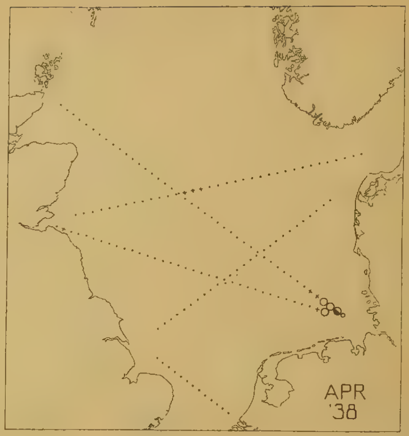
PLATE XXXVI

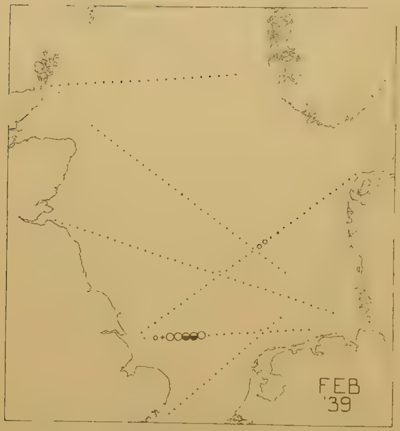
BIDDULPHIA AURITA

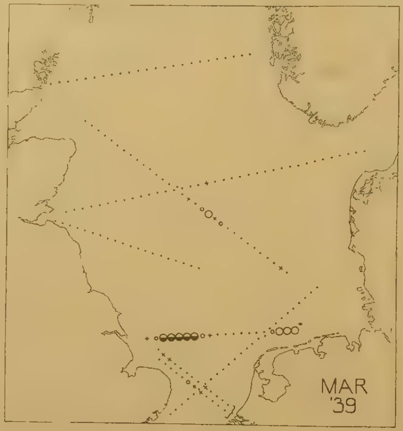
PER MILE
PER BLOCK

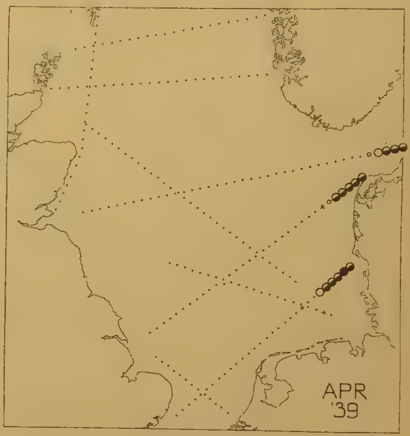
• = 0
+ = <5
∘ = 5-15
○ = 15-70
◒ = 70-700
● = >700
} X 100







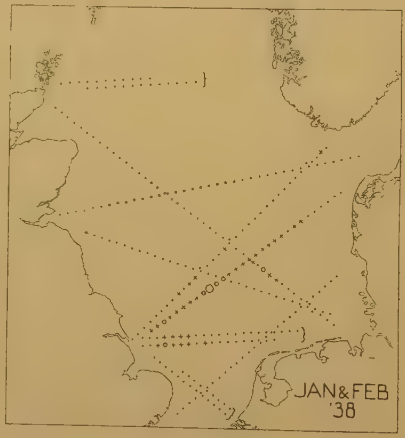


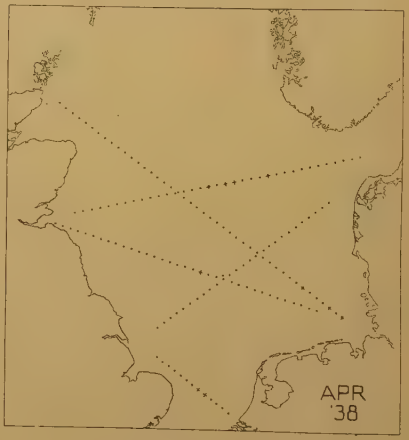


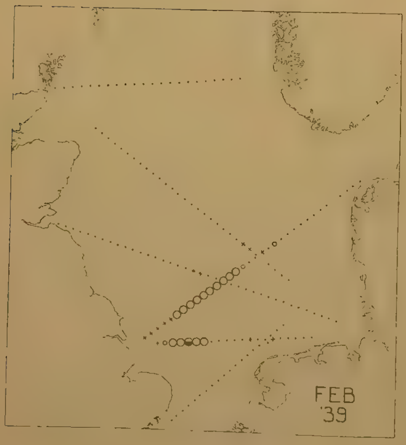
"NAVICULOID" DIATOMS

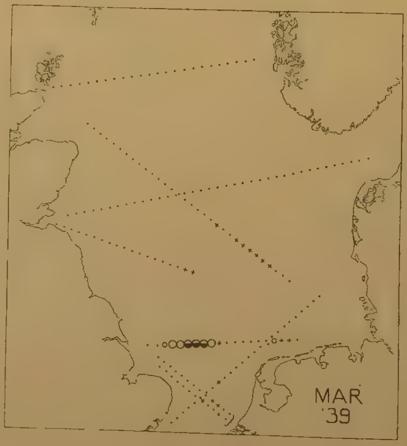
PER MILE
PER BLOCK

∘ = 0
+ = <5
∘ = 5-15
○ = 15-70
◒ = 70-700
} X 100









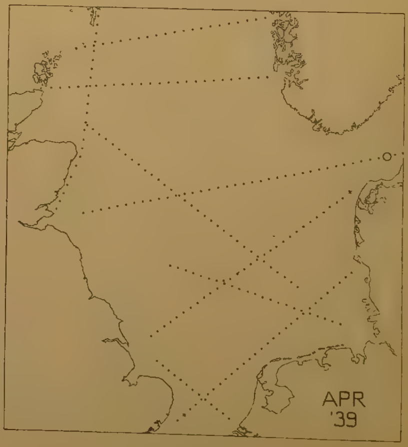
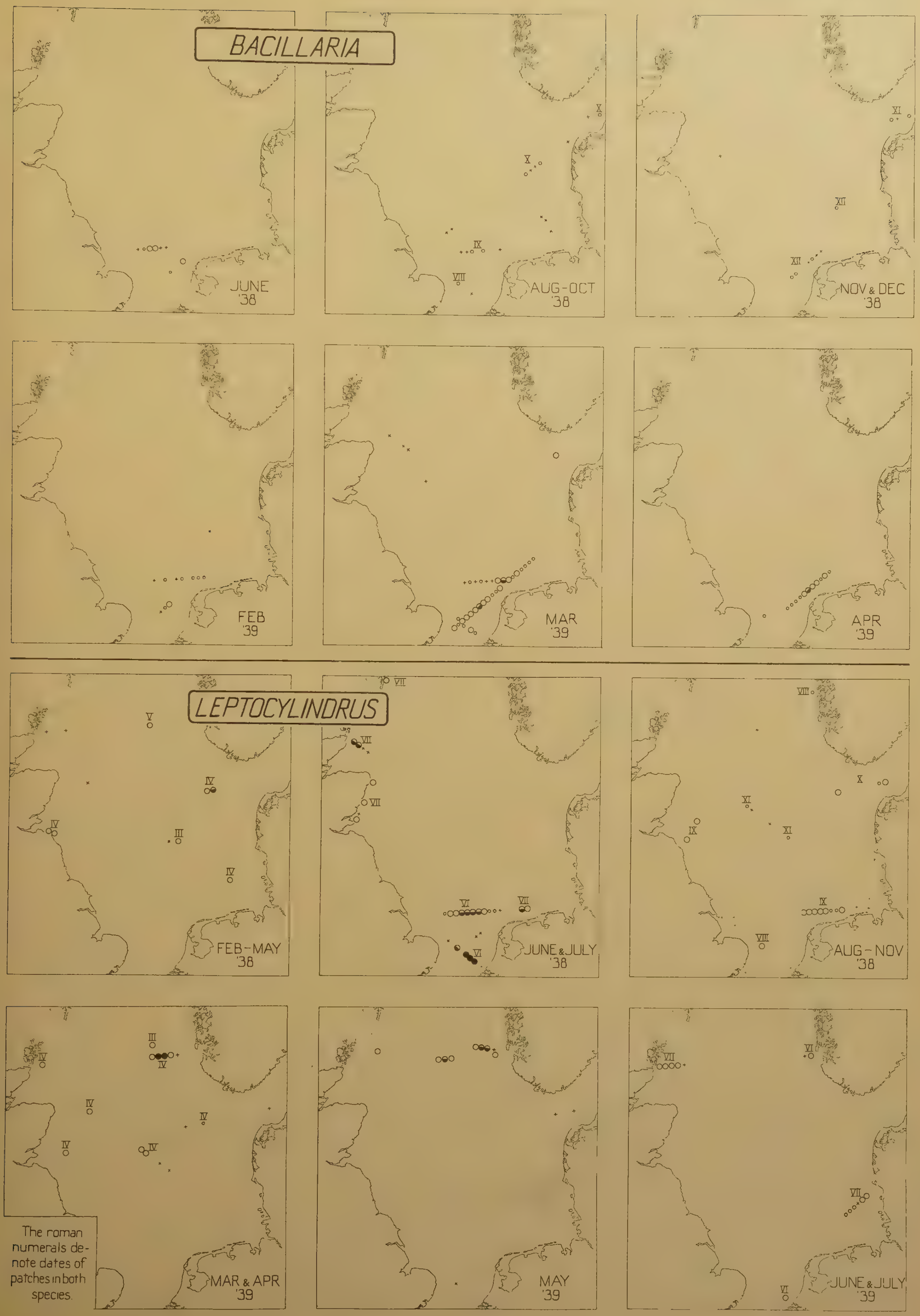
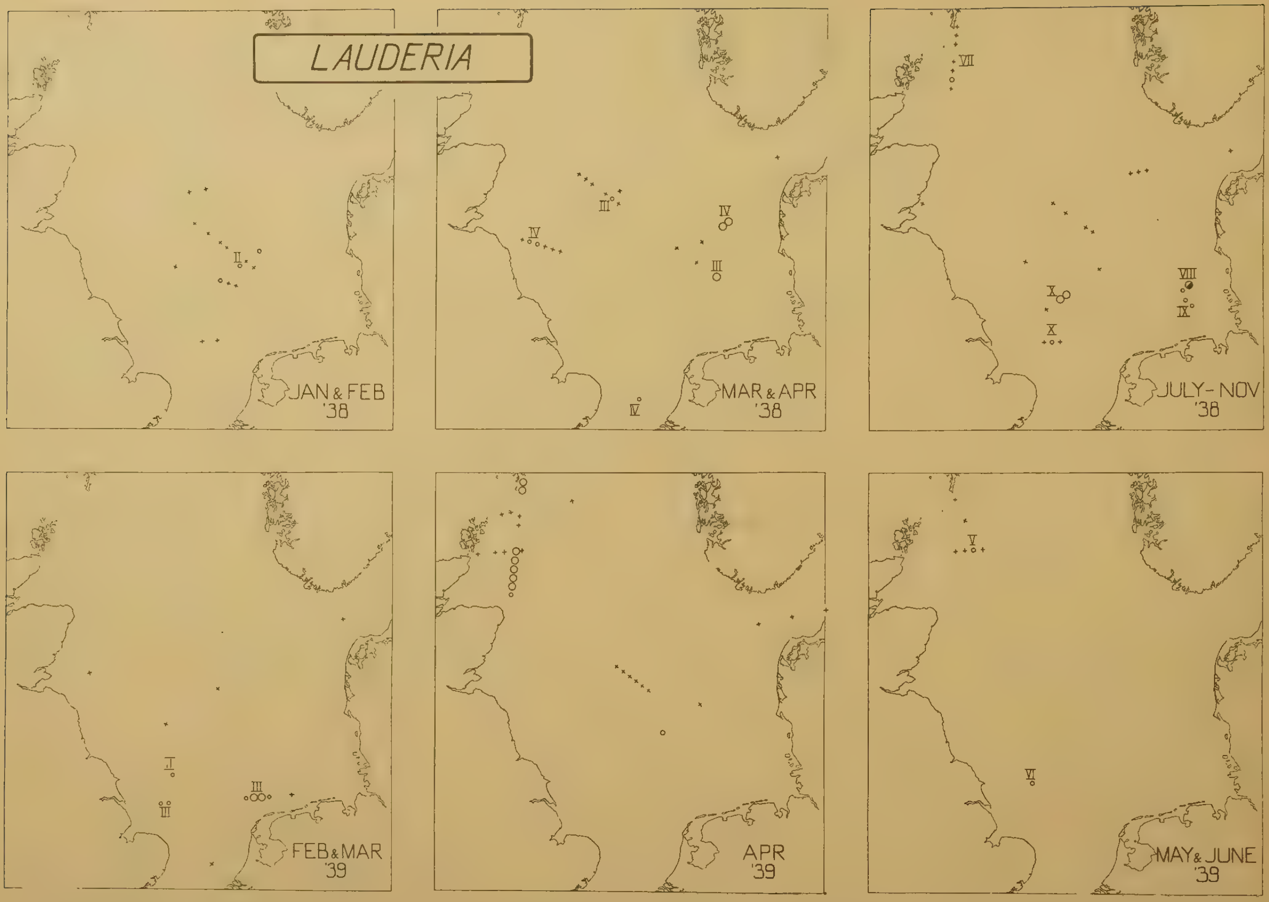


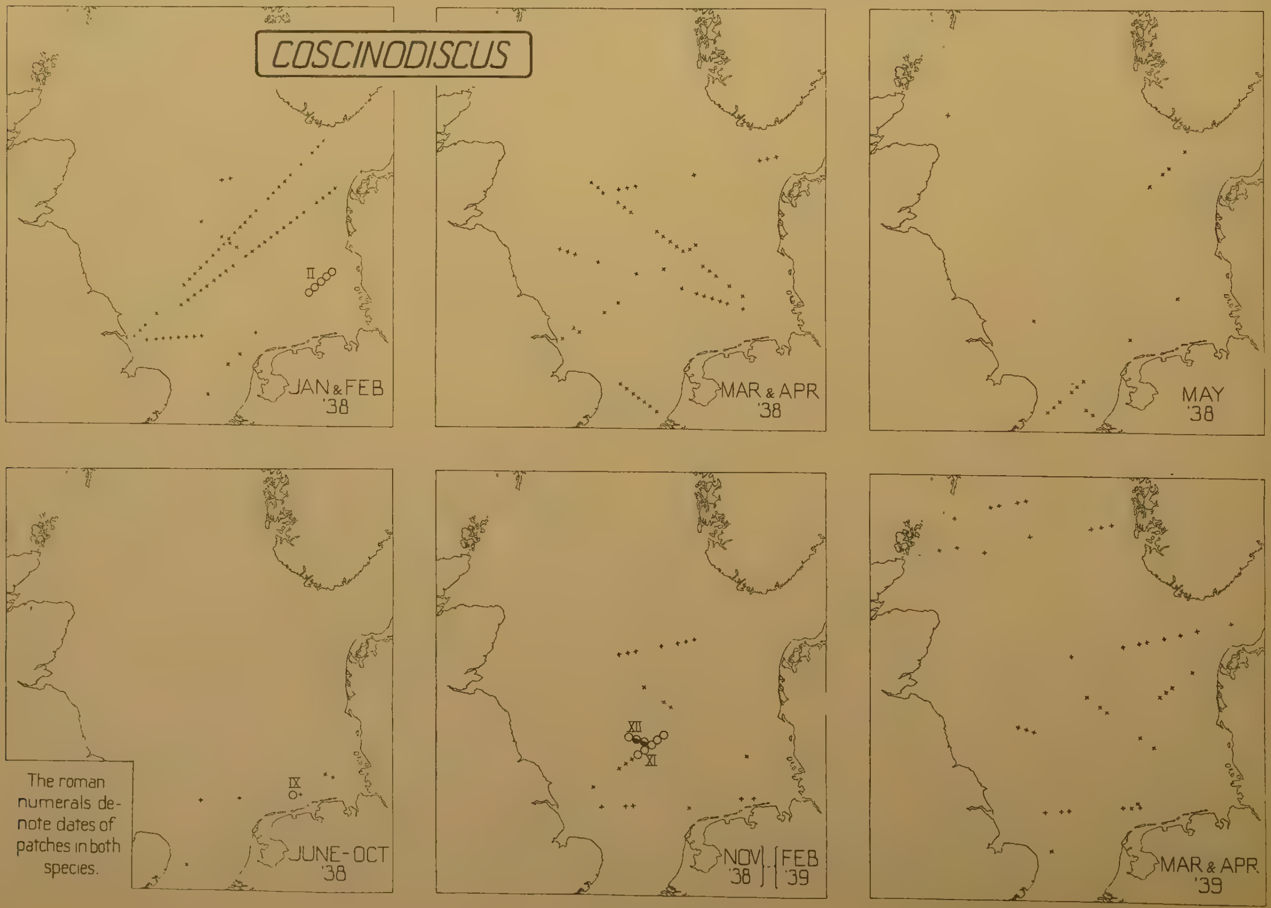
PLATE XXXVII


BACILLARIA
JUNE '38
X
X
IX
VIII
AUG-OCT '38
XI
XII
XII
NOV & DEC '38
FEB '39
MAR '39
APR '39
LEPTOCYLINDRUS
V
IV
IV
III
IV
FEB-MAY '38
VII
VII
VII
VI
VI
JUNE & JULY '38
VIII
X
XI
IX
XI
IX
VIII
AUG-NOV '38
III
IV
IV
IV
IV
IV
IV
MAR & APR '39
MAY '39
VII
VI
VII
VI
JUNE & JULY '39

The roman numerals denote dates of patches in both species.

PLATE XXXVIII


LAUDERIA
JAN & FEB '38
MAR & APR '38
JULY-NOV '38
FEB & MAR '39
APR '39
MAY & JUNE '39


COSCINODISCUS
JAN & FEB '38
MAR & APR '38
MAY '38
JUNE-OCT '38
NOV '38 | FEB '39
MAR & APR '39
The roman numerals denote dates of patches in both species.

[*Hull Bulletins of Marine Ecology, No. 9, Vol. II, pp. 47–70, Plates XXXIX–LXII, April, 1942.*]

CONTINUOUS PLANKTON RECORDS:

PHYTOPLANKTON IN THE NORTH SEA, 1938–39

PART II.—DINOFLAGELLATES, PHAEOCYSTIS, ETC.

BY

C. E. LUCAS, B.Sc.

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INTRODUCTION: MATERIAL AND METHODS.

The present paper deals with the flagellate data corresponding to that for the diatoms in 'Bulletin' No. 8 (Lucas, 1941). Publication was postponed a little for reasons of economy, but the two papers should be read in close conjunction in order to see the development of these two phytoplankton groups in relationship.

The results are based on a series of continuous records over the North Sea for twenty months from January, 1938, to August, 1939, inclusive, when the onset of the war prevented further work at sea. The extent of the sampling is shown in Plates XLVIII–LI in this paper, for example, whilst details regarding each record can be found in 'Bulletin' No. 7 (Hardy, 1941, Plates I–V and Record list). The general methods of investigation were similar to those for the diatoms. In brief the method of presentation involves the use of symbols to represent the quantities per mile found on each ten-mile block, in place of the graphical system of 'Bulletin' No. 3 (Lucas, 1940; see also Lucas, 1941, pp. 21–22). The data are shown on a series of monthly charts, whilst the usual descriptive part of the text is limited to points of emphasis and remarks concerning any data omitted from the charts for reasons of economy. The whole is reviewed in the general discussion relating these results to earlier ones and to those for the diatoms in 1938–39.

I should like here to express my thanks to Mr. W. Macnae, who analysed the bulk of the southern material but was unable to assist in writing up the data owing to his departure to take up other work.

DISTRIBUTION OF THE DINOFLAGELLATES.

It will be remembered that in the earlier work (Lucas, 1940) the Dinoflagellates were usually treated as a whole, although in the later years the groups *Ceratium furca* (+ *C. lineatum*) and *C. fusus* were separated from the rest. At the beginning of the present survey we decided to attempt a more detailed analysis of the whole group. The results are shown for the different species (or combinations of species) in Plates XL–LXII. We have not felt it justifiable to include also charts showing the distribution of the whole group, but for continuity, and in view of certain similarities in the main features of the distributions of the different species, the notes concerning these will be preceded by a generalized account of the group as a whole, together with derivative diagrams.

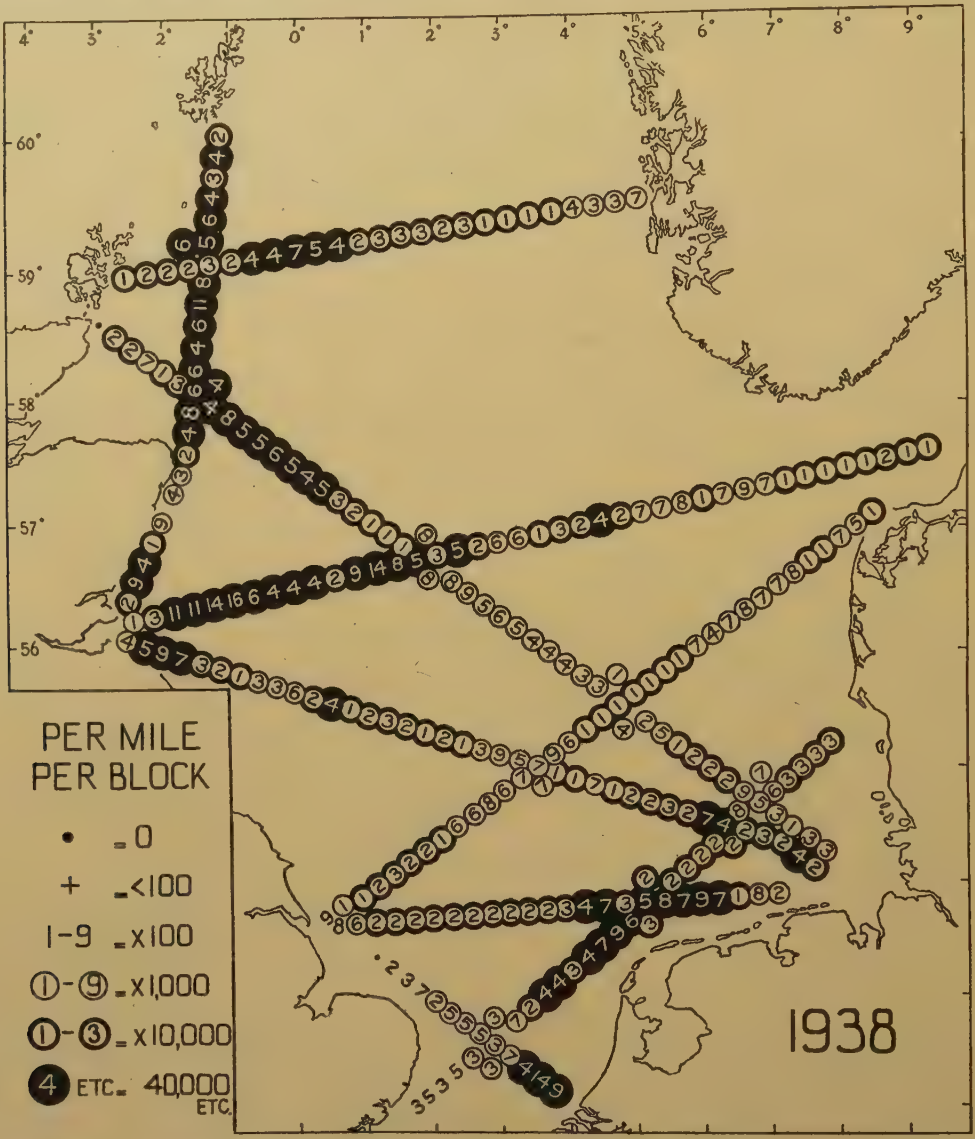
Two types of scale were used for the Dinoflagellates in the earlier survey; a simple linear scale was used for the whole group and a modified scale (similar to that for the diatoms) for the two species *C. furca* and *C. fusus*. In comparing the present data for the individual species with the earlier observations this point should be kept in mind. Comparison between the old scale and the new symbols has already been made (Lucas, 1941, where Text-fig. 1 shows the two methods side by side) and can be seen also in Text-figs. 1 and 2 here.

Reference has generally been made to Lebour (1925) for the identification of the Dinoflagellates, whilst Jörgensen (1911*a*) has also been used (see, however, notes on the individual species).

The January and February records in 1938 suggested the presence of a residual population from 1937, situated mainly on the eastern end of the Hull-Bremen line, although at least in February (when probably the numbers were decreasing) there was also a scattered growth over the central area and the Heligoland Bight. The scanty records for March, taken with the more numerous April records, suggest a mainly central distribution, exceptionally few cells being found in the north-western area and in the Southern Bight. These early results appear to show continuity with those for the previous December in the southern area (Lucas, 1940, Plate LVII), when we found the chief concentration off the Friesian Is. and over the Dogger Bank. In particular we may note that *Ceratium fusus* was the chief constituent at first (*loc. cit.*, Plate LXIV and Plate XLIV here). The numbers seem to have decreased until the end of February and, judging by the evidence of the Pentland-Hamburg line, probably increased again in March. Certainly the April numbers showed a marked increase over February in the central waters and, where there is comparable data, over March ; in addition they appeared to extend a little further towards the north-west.

It is important to remember here the associated diatom patches. During this time the principal spring diatoms had attained large numbers in the south and by May some were decreasing (Lucas, 1941, p. 37). The Dinoflagellates, on the other hand, then began to increase more rapidly. For the first time appreciable numbers appeared on the Rotterdam line as well as further north. It is likely that the first significant numbers to appear in the north-west were also in May, although the data for comparison is not very satisfactory ; these values, however, were much lower then than those in the south, and all the evidence suggests that development was about a month later in the northern waters as with the diatoms. Another interesting feature concerns a sparse area probably initiated in May over the western Dogger Bank. From February to April the Dinoflagellates had been fairly evenly scattered over the central waters (the higher values being found on the Hull-Copenhagen line in April). In May, however, whilst they were more widespread and numerous generally there was a decrease in numbers over this area. Further, it is difficult to avoid the conclusion that a similar but wider area of low values in June and July (when in most other places the numbers were still increasing) was an extension of the process first noted in May. The effect varied in the different groups, but the net result was an area of relatively, and often actually, lower values over the whole Dogger region and some of the waters to the north of it, signs of which were found in the earlier survey (e.g. Text-fig. 12 in "Bulletin" No. 3). It may be remembered that after the diatoms had first appeared in abundance in the central area, they too became relatively scarcer there (Lucas, 1941, p. 39).

The maximal numbers for most parts of the area were found in June or July (*cf.* Text-figs. 1, 2 and 3). Characteristically the greatest numbers were found in the north-west and off the Dutch-German coast. We can, in fact, distinguish two areas of production : a south-eastern one, appearing first, and a later but more extensive one off the east coast of Scotland, the Orkneys and Shetlands. In addition to these areas, the coastal zones in general stand out as being denser in relation to the lower values in the central area. More detailed examination of the north-western area gives some evidence for considering it as two dense areas separated by a less dense zone. These occupy approximately the Orkney-Moray

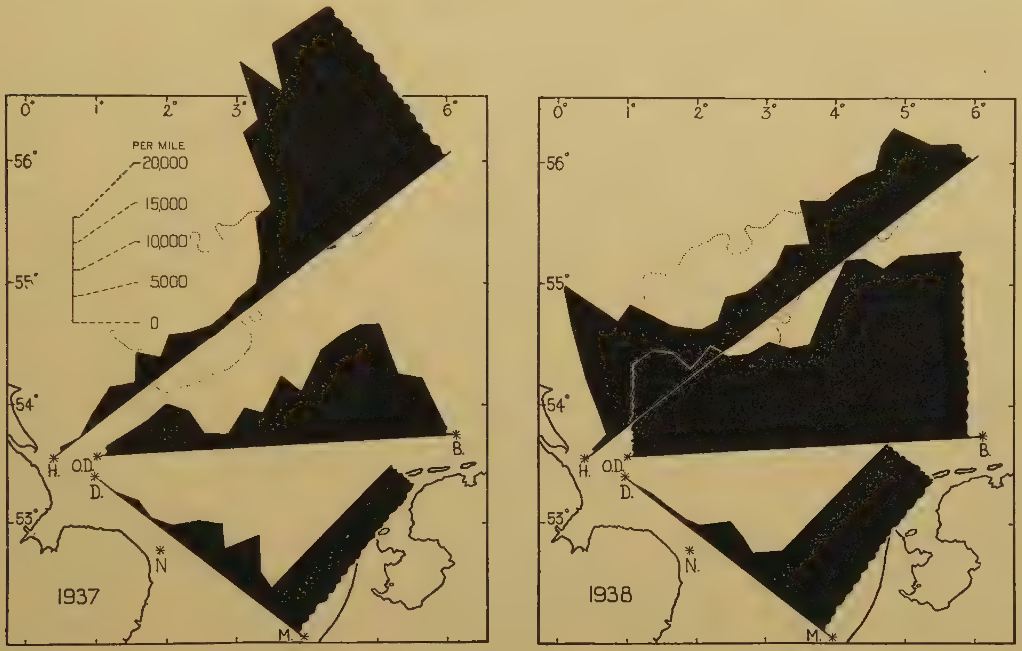

4°
3°
2°
1°
0°
1°
2°
3°
4°
5°
6°
7°
8°
9°
60°
59°
58°
57°
56°
PER MILE
PER BLOCK
• = 0
+ = <100
1-9 = x100
①-⑨ = x1,000
①-③ = x10,000
④ ETC. = 40,000 ETC.
1938

Text-fig. 1.—Chart showing the maximal quantities of Total Dinoflagellates recorded on the standard North Sea routes during 1938. Each symbol denotes the maximal number per mile found on each ten-mile block (see scale). Slight deviations from the normal routes have been approximated to the standard route for convenience, but the major exceptions (*e.g.* that for the Bergen line in December, 1938) have been omitted in order to prevent seasonal bias.

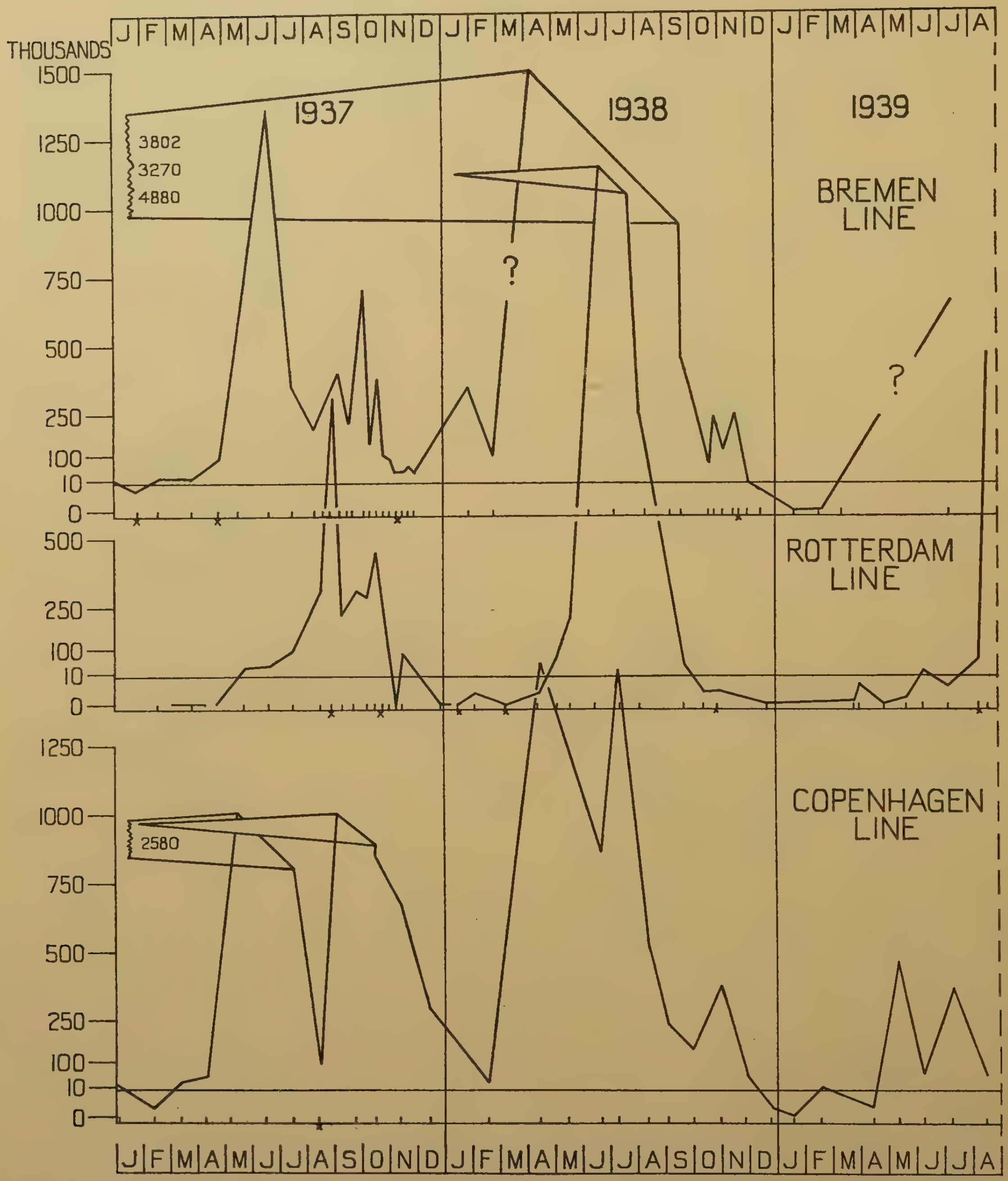
Firth area and the waters of the Forth–Tay region and are seen to have rather different constitutions.

From July onwards there was a progressive decrease in numbers on the whole.

The main centres were still in the north-west and the south-east, but by August the Shetland waters were sparser, whilst numbers off the Forth–Tay region were rather higher. As the numbers decreased further in September and October, there occurred a reversal of the process noted in the spring. The numbers decreased greatly in the north-west and the Southern Bight, whilst quantities in the central waters increased both relatively and actually. There are signs of a connection between some of the central patches in October and the earlier patches off the coast of Scotland, leading in turn to the November conditions when the few small patches of Dinoflagellates were mainly to the east of the October ones. In addition there was a fairly discrete patch to the south of the Dogger Bank, probably associated with the more extensive patches there in October. In association with this general decrease, the corresponding increase of diatoms such as *Rhizosolenia styliformis* will be recalled (Lucas, 1941, p. 37). By December the numbers were very low and mainly within the south-eastern waters once more. For the year 1938 some of the results are summarized in Text-fig. 1, showing the maximal values for the whole area in symbols, whilst for the southern area Text-fig. 2 shows similar data from the three southern lines in graphical form, which may be compared with similar graphs for 1932–37 in Text-fig. 12 of ‘ Bulletin ’ No. 3. The north-western and south-eastern areas stand out clearly from the rest, as also does the



Text-fig. 2.—Charts showing the maximal quantities of Total Dinoflagellates in numbers per mile (scale inset) recorded in the years 1937 and 1938 at different points along the three lines from Hull to Bremen, Rotterdam and Copenhagen. These should be compared with similar charts for 1932–37 in Text-fig. 12 of ‘ Bulletin ’ No. 3.



TEXT-FIG. 3.—Graphs showing the fluctuations in the total numbers of Dinoflagellates recorded between January, 1937, and August, 1939, for comparison with Text-fig. 11 of 'Bulletin' No. 3 (1932–37). The records for the Bremen line (between Outer Dowsing and Borkum light-vessels), the Rotterdam line (between E. Dudgeon and Maas light-vessels) and the Copenhagen line (from Humber light-vessel for 250 miles towards Hanstholm) are shown separately. Above and below are time scales in months; J.F.M., etc. Each point on a graph represents the total number of cells found on one record; the exact position of each record in relation to the time-scale is relatively sparse central area and the remaining coastal waters with more intermediate numbers. There is, however, a very sparse coastal area from the Humber southwards and a zone of low numbers off the west coast of Norway. Text-fig. 3 shows the total numbers of Dinoflagellates found on each record for the three southern lines, and may be compared with Text-fig. 11 in the report on the earlier survey.

As in the diatoms, there is a general resemblance between the data for the available eight months of 1939 and those of 1938; but there are also striking differences. One difference noted for the diatoms is even more marked here: this concerns the extreme scarcity in the south compared with 1938. After making full allowance for the omission of records in some months (due to ships being taken off service as the result of international conditions), the difference is still marked, in particular over the south-west quarter.

Only a few cells were found in January and February, 1939 (scattered over the eastern and central waters). Although they had increased a little in March, they were still few and principally in the east. There is a resemblance to 1938 in that the south-eastern growths appeared before those in the north-west. On the other hand, small numbers appeared in 1939, not only all along the eastern shores of the North Sea, but even off the Orkneys, where no Dinoflagellates were found by us in 1938. The difference is clearly shown on that part of the Pentland–Hamburg line north of 57° N. during the month of April in these two years. No Dinoflagellates were found there until May in 1938, but some appeared in March, and fair numbers in April, 1939. In fact, the northern area as a whole was the richest for most forms in April, 1939, although *Ceratium fusus* was also thinly scattered off the German coast.

The northern waters were again richly populated in May and June, the numbers in May being unusually high off Norway. In contrast to this the western region, from the Firth of Forth southwards, was relatively thinly populated. As a whole the numbers were still increasing, and continued to do so in July and August, one or other month providing the maximal numbers found for the different groups (and probably the highest for the year). Then the chief area was in the north-west, although the numbers off the Dutch coast (mainly *C. fusus*) were also quite high. In the poorer south-western quarter there were particularly low numbers over the south-west Dogger Bank and in the Southern Bight (again excepting the patch of *C. fusus* found in August). Except in so far as these lower numbers tend to mask the effect, we may note

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shown as a small vertical line against the base-line of the graphs. The scale of numbers is in thousands of cells per record; it should be noted that the vertical scale has been exaggerated below the 10,000 point in order to magnify the small, but often significant changes which occur when these flagellates are scarcer. The true base line, however, is also shown (*i.e.* just below point "10" on the scale). Records covering less than half the standard distance (see above) have been omitted except where indicated by an open circle; records covering less than 80 per cent. are indicated by an ×. The very high peaks are folded over to the left for space economy.

again the relatively smaller numbers in the central waters during the later months, recalling the more or less " barren " area there in 1938.

In the absence of data for the later months the maximal values for 1939 have not been shown for comparison with Text-fig. 1, but we can say that each month of 1939 showed fewer numbers as a whole than in 1938 (see also Table I). The denser patches, *i. e.* those showing over 1000 cells per mile per block for any species (numbers in circles), were scarce until May in 1939, although widespread in 1938 in April. In May, 1939, the bulk were in the north-east, instead of being more central, whilst the north-western numbers were higher than in 1938. Again, the June values over 1000 cells were limited to the northern half in 1939, whilst even in July and August there were still relatively few scattered over the southern half of the area, with the exception of *C. fusus*, which in turn was by no means as abundant as in 1938.

This southern scarcity in 1939 is reflected in Text-fig. 3, where the " total " numbers of Dinoflagellates on each record have been shown for the three standard southern lines in comparison with similar data for 1937 (see also Lucas, 1940, Text-fig. 11, and p. 65 here). Wherever comparable data are available the reduction after 1938 is quite striking. These graphs bring out another point to which we have referred in the earlier work. The Hull–Copenhagen data for both years show two distinct peaks in the totals, with lower numbers in midsummer ; similar changes were found in several earlier years. Although sometimes (as in 1934) similar peaks had also been seen on the Hull–Bremen line they have been less evident in the past, and there was little sign of them in 1938 or 1939 as far as records are available. It is not likely that the appearance of one dominant peak in 1938 is due to missing records. The rather irregular peak of 1938 would seem to correspond more to the earlier and dominant one of the previous years, in spite of the absence of some records in the spring, whilst there appears to have been quite sufficient sampling in the late summer and autumn to show ample signs of a later or " secondary " peak if it had been present. In no year have such double peaks occurred on the Rotterdam line. It thus appears that the " bimodal " sequence becomes more evident as one moves from the Southern Bight. Whilst it does not seem necessary at this stage to show similar graphs for the other routes, or for the individual species (for which see Table I), examination of the monthly records shows that this sequence was most marked in the central area, and that in the north-west again there is only one major peak.

The significance of these variations cannot clearly be seen now, although the distribution of the different species may throw further light on it. It was shown (Lucas, 1940, p. 143) that on the Bremen line *Ceratium fusus* may have played a part in the formation of the " secondary " peak. It can now be seen that other species may play their parts also, as they evidently did earlier on the Copenhagen line (see Table I). Here we should point out that this variation may not be unconnected with the varying importance of the central and the coastal waters (see p. 51).

TABLE I.—*Showing the Total Numbers, in Thousands, of Ceratium spp., etc., found on each Record taken along the Bremen Line* (B: *Outer Dowsing to Borkum L.V.*), *Copenhagen Line* (C: *From Humber L.V. for* 250 *miles towards Hanstholm*), *and Rotterdam Line* (R: *E. Dudgeon to Maas L.V.*) *during* 1938 *and* 1939.

Route.	Date.	*Ceratium* spp.							Other Dino-flagellates.	Total Dino-flagellates.
		furca.	*fusus.*	*tripos.*	*macroceros.*	*horridum.*	*longipes.*	*lineatum.*		
B.	1938.									
	26.i	99	200	13	36	6	4	0	0	358
	23.ii	34	35	10	19	2	0	0	0	100
	8/9.vi	526	1120	335	319	943	540	9	10	3802
	6.vii	401	1353	348	169	95	904	0	0	3270
	9/10.viii	168	2613	455	140	152	1254	15	83	4880
	6/7.ix	183	1934	407	221	144	164	0	0	3053
	20/21.x	47	325	55	17	5	6	0	0	455
	19/20.x	8	20	28	10	5	+	1	0	72
	25/26.x	37	89	44	15	27	+	27	0	239
	2/3.xi	32	49	10	9	14	6	5	0	125
	16/17.xi	16	123	26	4	52	+	31	0	252
*	22/23.xi	32	81	20	4	26	0	2	0	165
	30.xi/1.xii	+	8	2	1	0	0	0	0	11
	14/15.xii	0	7	0	0	0	0	0	+	7
B	1939.									
	20/21.i	0	+	0	0	0	0	0	0	+
	17/18.ii	+	0	0	0	0	0	0	0	+
	11.iii	+	24	0	0	0	0	0	0	24
	8/9.vii	57	156	240	20	161	24	0	0	658
C	1938.									
	19/20.ii	11	7	2	7	2	2	0	0	31
	15/16.iv	638	163	48	259	25	402	0	2	1537
	14/15.v	504	191	111	191	45	217	0	2	1261
	25/26.vi	354	40	86	238	0	136	+	2	856
	9/10.vii	325	114	172	355	80	466	0	+	1512
	12/13.viii	57	46	254	70	14	94	1	+	536
	3/4.ix	32	79	102	20	6	3	0	0	242
	1/2.x	36	28	58	6	20	+	0	0	148
	29/30.x	112	116	79	41	23	0	2	+	373
	26/27.xi	13	25	20	+	0	0	0	0	58
	24/25.xii	3	1	0	0	+	0	0	0	4
C	1939.									
	21/22.i	+	1	0	0	0	0	0	0	1
	18/19.ii	1	6	0	0	5	+	0	0	12
	15/16.iv	1	2	0	1	0	+	0	0	4
	13/14.v	14	14	+	28	0	378	1	20	455
	10/11.vi	15	6	3	19	12	4	0	1	60
	8/9.vii	61	76	51	24	7	126	3	5	353
	19/20.viii	1	54	+	5	0	0	0	0	60
R	1938.									
*	19/20.i	0	0	0	0	0	0	0	0	0
	2/3.ii	0	3	0	0	0	0	0	0	3
*	5/6.iii	0	0	0	0	0	0	0	0	0
	13/14.iv	+	4	0	0	0	0	0	0	4
	4/5.v	7	41	1	7	0	11	0	0	67
	18/19.v	49	115	9	10	6	29	1	1	220
	15/16.vi	36	1590	1	5	22	21	0	0	1675
	13/14.vii	0	2422	1	0	0	0	0	0	2423
	3/4.viii	+	949	0	0	0	0	0	0	949
	21/22.ix	+	30	0	0	0	0	0	0	30
	12/13.x	0	4	0	0	0	0	0	0	4
*	26/27.x	0	4	0	0	0	0	0	0	4
	21/22.xii	0	0	0	0	0	0	0	0	0
R	1939.									
	22/23.iii	0	1	0	0	0	0	0	0	1
	29/30.iii	0	7	0	0	0	0	0	0	7
	26/27.iv	0	0	0	0	0	0	0	0	0
	20/21.v	0	2	0	0	0	0	0	0	2
	8.vi	3	12	0	1	0	3	0	0	19
	5/6.vii	0	4	0	0	0	2	0	0	6
*	9/10.viii	+	61	0	0	0	0	0	0	61
	16/17.viii	3	1168	1	0	0	2	0	0	1174

* Denotes a record of more than one-half but less than four-fifths of the normal distance concerned (see Text-fig. 3).

One of the objects of the new survey was to obtain more information regarding the constituent species of Dinoflagellates (*cf.* ' Bulletin ' No. 3, p. 141). As a first step towards this it seemed suitable to choose first the group Ceratium, which comprises such a large proportion of the whole. The difficulties of identification for the non-specialist, even within this one genus, are well known (*cf.* the more or less continuous variation in the *Ceratium macroceros-horridum-longipes* series). In practice it was not possible to achieve complete separation and they have been grouped into *Ceratium furca* (Ehrenberg), *C. fusus* (Ehrenberg), *C. macroceros* (Ehrenberg) Cleve, *C. tripos* O. F. Müller, *C. horridum* Gran, *C. longipes* (Bailey), and a group *C. lineatum* (Ehrenberg), etc. Of these the first two are definitive. *Ceratium tripos* is nearly so, but under this head have been included the very few *C. bucephalum* (Cleve) which have been found (see p. 60). *Ceratium macroceros*, *C. horridum* and *C. longipes* are likely to be somewhat indeterminate in the limiting cases where the respective series may merge (*cf.* Gran, 1902) ; as far as possible the standards set up by Jörgensen (1911*a* and 1920) have been used here. *Ceratium arcticum* (Ehrenberg) Cleve, which may also belong to this series, has not been found according to our determinations. Although it is usually possible to separate *C. lineatum* from others which resemble it to some extent (*e. g. Ceratium minutum* Jörgensen and the heteromorphic forms of other species, such as *C. tripos*), yet this was not practicable when these were most abundant, and consequently most important. In view of this the whole of these have been included in the group *C. lineatum*, etc. In addition to these a few cells of *C. lamellicorne* Kofoid were seen.

For a short time in 1939 *Prorocentrum micans* (Ehrenberg) was found and was easily separated. It has been fairly common to find moderate numbers of Peridinium spp. and Goniaulax, etc. ; owing to the difficulties of separating these in the time available they have been combined in a group Peridiniidae (less Ceratia). Of the other Dinoflagellates the Dinophysidae were fairly common, determination being limited to the family. In addition occasional specimens of the crescent form of *Gymnodinium lunula* Schütt have been found.

In general the different Dinoflagellates have a rather similar distribution, so that it is possible to speak of Dinoflagellate areas in which many of the species are present in large numbers at the same time. Yet this must be qualified. Some are much more abundant than others and, although this may be in part due to differential sampling (size and shape differences), it is still partly due to significant natural differences in proportions. It is difficult to say how far the first or the second factor has been the more important. It is well known that collecting by nets may variously modify in the catch the proportions of the different forms naturally occurring in the sea, fine nets catching a larger proportion of the smaller forms than coarse ones. For this reason the mesh employed here, 60 meshes to the inch, should clearly result in a smaller proportion of, say, Peridinium spp. in comparison with *C. macroceros* than may actually occur in the water (the mesh in fact is such that a serious but varying proportion of *all* these forms is likely to be lost). In order to assess such differential loss it would be desirable to contrast these results with comparable ones taken with a fine net, or with a water bottle. Whilst samples of this type may be available from earlier work, they cannot be directly compared with the present material, and it has not so far been possible to provide comparative data from, preferably, water bottle samples taken approximately at the same time and place as Recorder samples. However, it may be useful to make an estimate of the proportions of the different species, etc., *in this material*, and the values below are based on the broad seasonal and spatial distribution over the whole area. In relation to *C. fusus* as 100, the other types could be represented approximately by numbers of the order of 25 (*C. furca*), 10 (*C. tripos* and *C. longipes*), 5 (*C. macroceros*), 3 (*C. horridum*), 1 (Peridiniidae except Ceratia), less than 1 (*C. lineatum*, Dinophysis spp., etc.). It must be emphasized that such figures are very approximate and have a significance directly limited to the recorder work. They show that it is not surprising that the apparent distribution of the whole group should be the result largely of that of *C. fusus*, which may dominate entirely. On the other hand, so great are the seasonal and temporal changes that, whilst at times *C. fusus* may be almost in the pure state, at other times the group may be dominated by some other form. In view of these factors the following notes are added to emphasize points concerning the respective distributions illustrated in Plates XL–LXII.

The charts of the individual distributions have had to be arranged rather arbitrarily. For each of the individual Ceratium spp. these have been grouped at six to the page for 1938 and the first six months of 1939. For economy, however, the six pairs of charts for July and August, 1939, needed to be grouped on two plates, each showing three pairs (*e. g.* Pl. LI). For the remaining Dinoflagellates and Phaeocystis we have selected the more significant months so that each form could be shown on one page only.

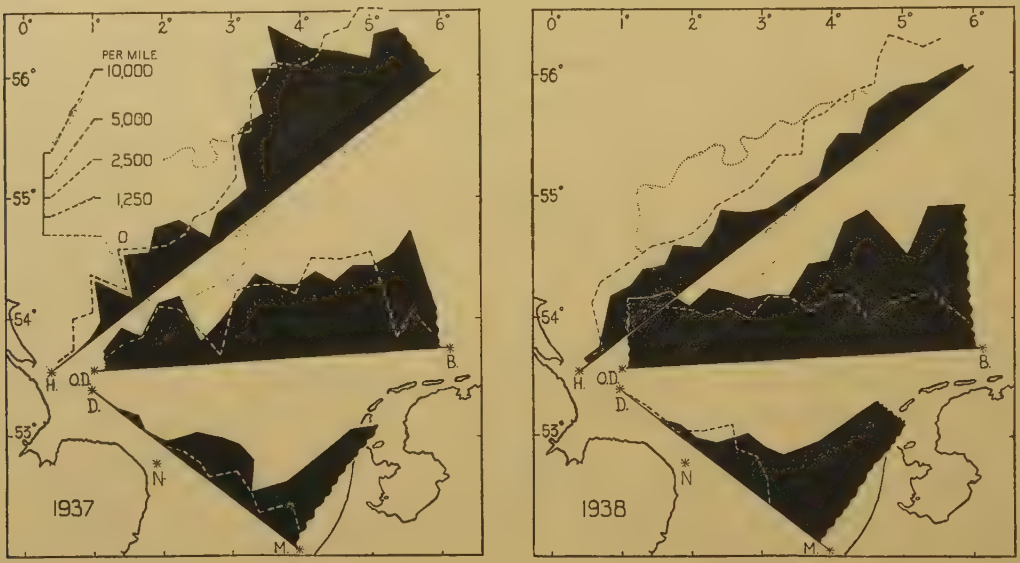
Ceratium furca (Ehrenberg). (Plates XL–XLII and LI.)

Maximal numbers were attained in July and August in both 1938 and the incompletely sampled 1939, but there were marked differences between them, much higher numbers being found in the north-east in 1939, as well as many fewer in the south and south-east. In fact, the numbers in the whole area were much lower in 1939 for each month, although this was less marked in the north, which in both years produced the largest and densest patches. In 1938 these were mainly off the Scottish Coast, numbers rapidly falling off towards the Shetland Is. and the Dogger Bank. Particularly sparse regions were found off Norway and at either end of the Rotterdam Line, whilst in 1939 almost the whole of the waters south of 56° N. Lat. were very thinly populated. Whilst there was a region of higher production in the south-east in 1938, this was small in comparison with the north-western one. Text-fig. 4 (broken line) shows the maximal values found on the southern lines in 1938 in comparison with those of 1937.

In general these records confirm and extend the findings of Jörgensen (1911*b*). One discrepancy seems worthy of note. He found *C. furca* still common in the north in November, whilst one of the striking features of our survey in 1938 was the rapid decrease of this and other forms of Ceratia after September, over a region which rapidly extended from the Scottish coast towards the east. The widespread southern scarcity in 1939 would also appear to disagree with his general findings.

Ceratium fusus (Ehrenberg). (Plates XLIV–XLVI and LI.)

This species shows a number of differences in distribution from *C. furca*. In 1938 the north-western maxima were found in June and July and the south-eastern in July and August, in spite of the fact that on the whole the population of the southern waters developed rather earlier than the northern ones. In 1939, again, they were similar, but the northern patches were distinctly thinner in the Firth of Forth region and extended rather more to the east this time. Similarly the southern patches developed rather later in 1939, *e. g.* they were decidedly thinner in June and less extensive in July (although in the Orkney-Shetland waters the numbers were rather higher this year). The striking feature is the reduction over the southern area as a whole and particularly in its western waters. As with all other Ceratia, it was much scarcer off the Wash and the Norway Coast at all times. These matters are important, since it will be seen that the distribution of *C. fusus*, owing to its unusually large numbers at most times, tends to determine the apparent distribution of the genus. It was remarkable in forming



Text-fig. 4.—Charts showing the maximal quantities of *Ceratium fusus* (blacked-in) and *C. furca* (broken line) in numbers per mile (scale inset) recorded in the years 1937 and 1938 at different points along the three lines from Hull to Bremen, Rotterdam and Copenhagen. These should be compared with similar charts for 1935–37 in Text-figs. 14 and 15 of ‘ Bulletin ’ No. 3.

almost " pure " communities in some places (*e. g.* off the Maas). Text-fig. 4 shows the maximal quantities (blacked-in) found on the southern lines in 1938, along with those for *C. furca* and compared with similar maxima for 1937.

Once again, the results may be said to agree largely with those of Jörgensen (1911*b*), although there is a discrepancy regarding his suggestion of a November maximum " in der mittleren und sudlichen Nordsee und im Skagerrak." According to our results in 1938, a limited region of the central and Skagerrak waters showed a peak in October and November, but another peak occurred there in May and June ; similarly the largest numbers in the Southern Bight and Heligoland Bight occurred in July, although we should bear in mind the large numbers of the previous January off Heligoland and the slight increase there again in December, 1938. Jörgensen commented on the extreme euryhaline nature of *C. fusus*, and this is well borne out when we consider that the largest quantities were actually found off the coast of Scotland and off Holland and Germany. Without going into details of hydrology at this stage (these will be dealt with in a later paper), it will be realized from general information that quite considerable contrasts in salinity may be expected in these waters.

Ceratium tripos O. F. Müller. (Plates XLVIII–LI.)

It is possible (see below) that very small numbers of *C. bucephalum* have been included with *C. tripos* owing to uncertainties of identification. For the species proper, the maximum numbers were found in August for both years and were almost limited to the north-western region, in contrast to the foregoing species, which also had significant numbers in the south-east. Whilst there were appreciable numbers there also, they were not distinguishable from the other moderate coastal growths. We should note that whilst in 1938 the north-western zone was extensive and fairly clearly subdivided into two sub-zones separated by a narrow sparser region off the Moray coast, in 1939 the area of similar density was much smaller, corresponding largely to the northern of the two former ones. Again we see the great decrease in the southern waters in 1939, and also that the northern waters were rather thinner : yet even in 1938 few were to be found as far south as the Rotterdam line.

This form was rather sparser than elsewhere off Norway in 1938. Here, however, we may note a point that is more evident in *C. tripos* than in some other species, *i. e.* that whilst there was a general reduction on approaching Norway (compared with the western numbers), yet as one comes still nearer to the coast there was often an increase again (*e. g.* June, 1938). There resulted normally a narrow channel containing the lowest numbers.

Whilst there is general conformation with Jörgensen (1911*b*) here, it is apparent that in 1938/39, at least, we could not support the implication (p. 218) that *C. tripos* is usually as numerous at the north Dutch stations as in the northern waters, nor that the central region is rich, since, as with most other species, *C. tripos* shows a tendency to be scarcer in the centre than elsewhere.

Ceratium bucephalum Cleve.

It is likely that occasionally very small numbers of *C. bucephalum* (Cleve) have been included with *C. tripos* owing to the uncertainties of identification. Such of these as have been identified as *bucephalum* with confidence have been found in the waters round the Dogger Bank (on the Bremen and Copenhagen lines), and although it is possible that others may have occurred elsewhere, the numbers have undoubtedly been remarkably small in view of Jörgensen's account. He found it particularly common in the German Bight and in the eastern waters generally (*i. e.* those regions in which we found *C. tripos* to be scarce or only moderately common). He mentions, however, finding it " in etwas tieferen Schichten " (*loc. cit.*, p. 222), which, in conjunction with his statement (p. 223) that " Die hohen sommer temperaturen scheinen wieder hemmend auf die Entwicklung zu werken," suggests that the recorder does not sample a deep enough layer to sample proportionate quantities of it (see also note under *C. macroceros*).

Ceratium macroceros (Ehrenberg) Cleve. (Plates LII–LIV and LIX.)

In 1938 the maximal numbers were found in the central waters in June and subsequently in German and Scottish waters. The numbers were much smaller in 1939, with a maximum in July and August, widespread in the former and restricted in the latter. Once again the striking feature was the low numbers throughout the south then, although they were also low south of the Hull–Bremen line in 1938. Like so many others, *C. macroceros* was also rather scarce off Norway, although showing occasional signs of increase very near to the coast.

It is interesting that Jörgensen should have drawn attention to a correlation between this species and *C. bucephalum*, which was so rarely seen by us. Another difference between our results and those of Jörgensen lies in his suggestion of a November maximum in the Scottish area, at a time when this and most other species there were very scarce in 1938. Along with a similar finding for *C. furca* this suggests some considerable differences between the results of 1938 and the earlier years. They agree however in that the present results for *C. macroceros* show a rather later maximum than for some of the other species, and it may be that his suggestion of November (with August secondary) is due largely to the use of merely quarterly surveys.

Ceratium horridum Gran. (Plates LVI–LIX.)

This comprises the northern section of the group defined by Jörgensen (1920) and, as used here, is liable to include a few debatable specimens of *C. longipes* (and *vice versa*). Future Continuous Recorder work might include fuller study of the relationships between these two, both in space and time.

This species was rather earlier than some of the others, the largest numbers being found in June and July in the north-west in both years and along the Hull–

Bremen line in June, 1938. Similarly it decreased again rather earlier. After the preliminary growths in the central waters it was particularly scarce there in 1938, and was even scarcer at most places south of Lat. 56° N. in 1939. Jörgensen comments on its great variability from year to year, and this may well account for some disagreement between our data and his. In this connection it is of interest that, unlike most species, this was definitely more abundant in the northern waters in 1939 than in 1938.

Ceratium longipes (Bailey) Gran. (Plates LX–LXII and LIX.)

Here, according to these results, the development was even earlier than with the last species. Even in May large numbers were to be found and, whilst scarcer in April, it was then the commonest form in the central waters. The true maximum, however, occurred in the south-east in July, 1938, and in the north-east from May to July in 1939. This is the biggest difference between the years which has been noted so far. In 1938 *C. longipes* was largely a southern form, whilst in the next year extremely few were found in the southern half of the North Sea and it was mainly a north-eastern species. In both years, in contrast to the species above, it was scarce in the north-western area, the only dense patches being found off the mouth of the Forth in 1938, where it was very scarce in 1939. Against this we see that almost the only appreciable patches to be found in August, 1939, were in the north-west, although these were very small.

Jörgensen noted the early development of this form, but also found it to be common in the Scottish area, with which our observations for both years disagree. On the other hand, he (and others) have commented on its cold-water affinities, and it is possible that it tends to lie in deeper layers than some of the other forms, consequently appearing less important in the Recorder collections over deeper waters. Such possibilities must be borne in mind, whilst remembering that the records still show the actual numerical relationships of the various species in a given layer of water at any time. Jörgensen has also stressed the need for investigation of the distribution of *C. longipes* and his *C. intermedium* (= *C. horridum* here). It may be significant that we have already noted *C. longipes* as the earliest of these Ceratia on the whole, *C. horridum* as rather early, whilst *C. macroceros* was one of the latest.

Ceratium lineatum (Ehrenberg), etc. (Plate XLIII.)

For reasons of economy, it has been necessary to show only representative charts of this and the next few groups. In addition to those shown for *C. lineatum* on Plate XLIII, there were other traces off the Forth in March and April, 1938, with scattered numbers off the Skagerrak in April. In October there were patches south of the Dogger Bank which persisted into November; no more were found until a few appeared north of Lat. 56° N. in March and April, 1939. The chief production was off the east coast of Scotland in both years, whilst numbers were, as usual, very low over the southern area in 1939.

Ceratium lamellicorne (Kofoid).

Whilst the few cells which appeared to belong to this warmer water species were hardly typical, they could not reasonably be placed in any other species. They appeared in the middle of the Leith–Lerwick line on 17th July, 1938. Jörgensen also notes its extreme scarcity, having found it no nearer the North Sea than off the mouth of the English Channel in 1908 and south of Faeroe in the same year. (See also note regarding *Dinophysis tripos* below).

Peridiniidae other than Ceratia. (Plate XLVII.)

In addition to those shown, small numbers were found in January and March, 1938, whilst in April they were scattered over the Dogger Bank and towards the Skagerrak. A few were left, mainly in the north-east, in October and November, after which none were found until March, 1939, off Bergen ; a few more appeared there in April, some in the centre and more off the Orkneys. The chief patches were off Heligoland, the Skagerrak and the east coast of Scotland in 1938. In 1939 they were very scarce south of Lat. 55° N., although fair numbers appeared then off Norway. There was a definite barren central area in 1938.

From time to time large numbers of Dinoflagellate cysts have been found, particularly off the east coast of Scotland. There is reason to believe that most of these belonged to this group.

Dinophysidae. (Plate LV.)

In addition to those shown, there were scattered occurrences in February, April, and from October to December in 1938, after which there were no more until May, 1939. It is likely that, as for most other Dinoflagellates, a relatively barren central area might be suggested, but this is less clear here owing to the very small numbers in the southern area in 1938 ; they were even scarcer there in 1939. The maximal area was off the Forth in both years. In the last year the patches occurred first in the east and then in the west.

It is of interest that a few cells of *Dinophysis tripos* Gourret were found off the Forth in September, 1938. The occurrence of this warm water form may be compared with that of *C. lamellicorne* above.

Prorocentrum micans Ehrenberg.

This was not recorded until 30th July, 1939, when a few were found off the Moray Firth. It is probable that this patch still existed in mid-August, since cells were found in the " Tank Residue " (see definition in Lucas, 1940, p. 75) of the Leith–Lerwick record for that period, although there is no record of its exact position. It is likely to be too small to be recorded regularly.

Gymnodinium lunula Schütt.

A few specimens of this species have been found from time to time, both in this and in the earlier work. During this survey they were principally in the north central waters and on the Leith–Lerwick line in July and August, 1939. Others occurred (*e. g.* off Heligoland) in May and July, 1938. Other "naked" Dinoflagellates have been recorded at times, but they are probably too delicate as a group to be recorded adequately.

DISTRIBUTION OF THE OTHER FLAGELLATES.

Whilst there have been signs from time to time of the large numbers of flagellates (Silicoflagellates, green and colourless flagellates, etc.) which other types of work have shown to be so important in the nannoplankton, most of them are so poorly sampled owing to their small size (and also damaged) that little of value could usefully be said of them with the exception of Phaeocystis and Halosphaera. These have been recorded in larger and more determinate quantities and are worthy of comment.

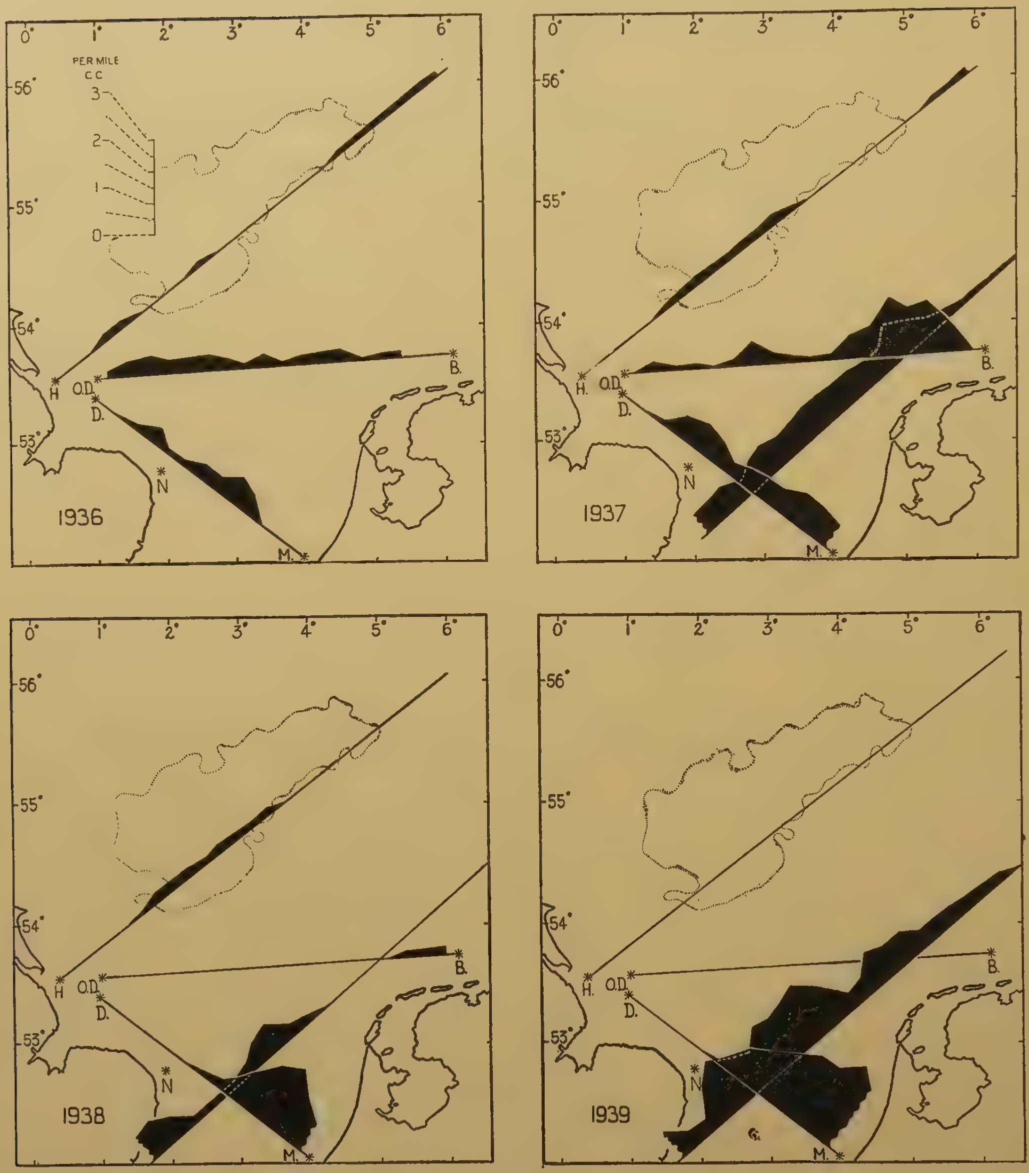
Phaeocystis. (Plate XXXIX.)

Except that, in agreement with other forms, symbols have now been adopted in place of the graphical methods of the earlier 'Bulletins,' the data for Phaeocystis have been dealt with as before (Lucas, 1940, p. 149). Nearly all the data is shown in Plate XXXIX. Other "significant" but very thin patches appeared off Borkum in September and in the central waters in November, 1938, but there were no "significant" quantities in any other months (see p. 149, *loc. cit.*, regarding the lower limits below which possible occurrences of Phaeocystis have been disregarded).

As we found for so many other organisms, the major concentrations were in the north-west and the south-east during the spring of each year. Of these the former was appreciably smaller, appeared rather later and decreased earlier in each year. At the same time there were much thinner central patches in both years, as well as smaller autumnal patches. In contrast to many other species there was a considerable increase in 1939 over 1938, not only in the north-west, but also in the south-eastern waters, where amongst the diatoms and the Dinoflagellates there were striking reductions in 1939. This is shown effectively in Text-fig. 5, where the maximal quantities found in the southern area for the two years appear side by side. In particular we may note that as far as evidence is available the patches in the Southern Bight were mainly along the eastern side in both years, the larger patches of 1939 extending a little further to the west than in 1938. It has not been possible to identify the species concerned.

Halosphaera viridis Schmitz. (Text-fig. 6.)

Halosphaera was not referred to in 'Bulletin' No. 3 owing to some uncertainty regarding its identity on the records. In their rather damaged condition it was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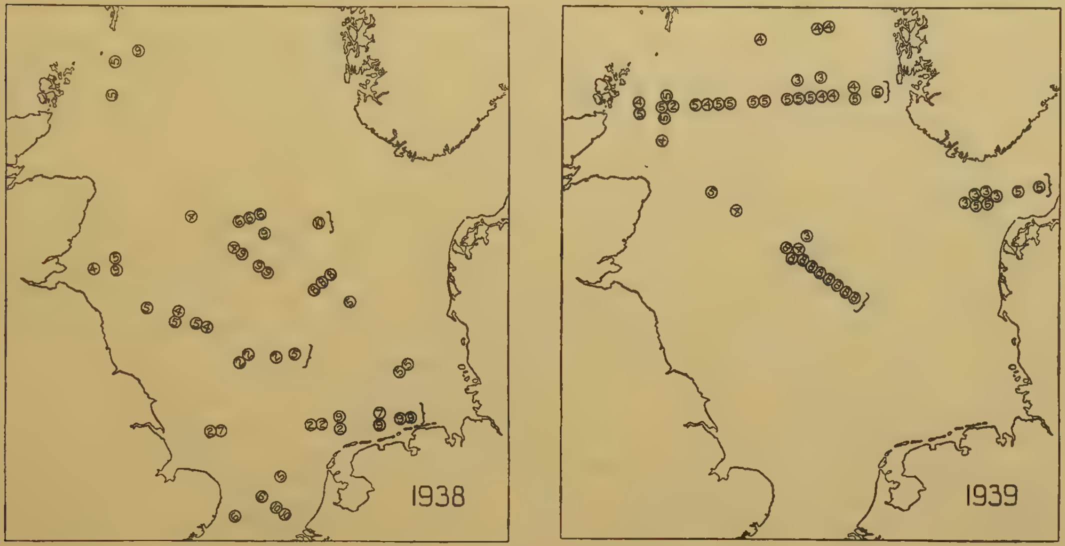
1936
1937
1938
1939

Text-fig. 5.—Charts showing the maximal quantities of Phaeocystis in c.c. (scale inset) during the years 1936–39 at different points along the three lines from Hull to Bremen, Rotterdam and Copenhagen. These should be compared with similar charts for the years 1932–37 in Text-fig. 16 of ' Bulletin ' No. 3. Note, however, that data for the Esbjerg line has been added here for the years 1937–39 : data from this line in 1936 and from the Bremen line in 1938 and 1939 were inadequate.

not possible to be sure at the time whether some of the flagellates were Halosphaera or not. Our more recent work in the central and northern waters of the North Sea has shown that Halosphaera withstands very well the effects of passing through the Recorder and that there can be few doubts about its identity. This enables us to say with certainty that it was scarce in our records during the years 1932–37. Whilst a few were found in the comparable area during 1938, the records in 1939 were mainly found north of Lat. 55° N. Nowhere could it be described as abundant, but May was apparently the maximal month in each year.



Text-fig. 6.—Charts showing the overall occurrence of Halosphaera in 1938 and 1939. The numbers within the circles (1–12) denote the months (January–December) during which Halosphaera was recorded on the different blocks.

Discussion.

Comparisons with the 1932–37 *Data.*

In view of certain similarities in the annual variations of the different members of the phytoplankton, it seemed more suitable to compare all the results for 1938 and 1939 with those for 1932–37 in one place rather than in the separate sections devoted to the different species. This will only be possible for the southern area, and principally for the three lines, Hull–Bremen, Hull–Copenhagen and Hull–Rotterdam, which were sampled more or less fully during the earlier years. In addition we can make use of the London-Esbjerg line for the year 1937 and part of 1936. Comment on the northern area will have to be limited to remarks for 1938 and 1939 where they seem relevant.

It will be remembered that as a group the Dinoflagellates showed lower numbers in 1933 (and to some extent 1934) than in 1932; they then variously increased until 1937, when they attained large numbers on all the southern lines. This is shown clearly in ‘ Bulletin ’ No. 3, text-figs. 11 and 12, where the “ maximal ” and “ total ” quantities on the three main lines are shown for each year. In order to continue this series, Text-figs. 2 and 3 here have been prepared in a similar manner to show the present data for the whole group in 1938 in comparison with that for 1937. Similarly we found that *Ceratium fusus* had increased over the last three years (and probably over a longer period), although this was not so for *C. furca* except on the Rotterdam line (Lucas, 1940, text-figs. 13 to 15). The “ maximal ” quantities of these two species for 1938 in comparison with 1937 are shown in Text-fig. 4 ; comparable data for 1939 are not shown, since the sampling was incomplete. It has not been thought necessary to give also the graphs showing the variation in “ total ” quantities for these two species (particularly as it is not possible to compare such with the 1937 data for other species), but the results for 1938–39 appear in Table I.

In all these forms quite striking changes may be seen in the later years. On both the Bremen and the Rotterdam lines the Dinoflagellates in 1938 showed increases over 1937, those for the Bremen line being very great, and those for both providing the largest numbers found on the lines during the whole period. On the Copenhagen line, however, there was a decrease in 1938, and it may be that this to some extent anticipates the remarkable decrease found on all the lines in 1939 up to August, as far as our evidence goes (Text-fig. 3 and Table I). The numbers on the Copenhagen line were reduced to values little over those of the scarce years 1933 and 1934. Unfortunately the evidence for the Bremen line is scanty, but such data as is available, borne out by the general scarcity on the neighbouring lines, suggests values of the order of those in 1933. Whilst the decrease is by no means so marked on the Rotterdam line, the maximal numbers found were much lower than those found up to the same dates in 1938. Similar decreases were found on the Esbjerg line. Not only were these decreases found in the whole group, but they appear to have applied to all the more abundant (and probably most of the less significant) species in each month for which data is available (Table I). In fact, as we have already noticed, only *C. fusus* was found in fair numbers in the south during 1939, and even these were much lower than in the previous year. In association with these changes, we should note that, whereas from 1932 to 1936 the Dinoflagellates tended to become more abundant in the west, yet in 1937 the bulk were definitely to be found in the east, and that they were similarly distributed in 1938 and 1939. They were rather more to the west in 1938 than in 1937, but the western ends of the three main lines were particularly thinly populated in 1939.

Phaeocystis showed a rather different cycle of changes. After being quite abundant until 1934, it was scarcer in 1935 and 1936, increasing again in 1937. In addition it was rather eastern in distribution for the first two years, then western until 1936, showing some return to the eastern condition in 1937 (Lucas, 1940, text-fig. 16). These results may be compared with the present Text-fig. 5 for comparison (data for the Esbjerg line being added for the years 1937–39). In 1938 there were similar quantities on the Copenhagen line to those in 1934–37, but in 1939 there was none, although in April there was a small patch to the north of this line. Volumes on the Rotterdam line in 1938 were rather higher than those of 1932 and 1933, whilst those of 1939 were a little higher still. Owing to the omission of data for the important spring months on the Bremen line, it is impossible to compare the results adequately with those of the earlier years. The graph for 1938 is based on the June data only, none being available for April and May, when Phaeocystis might have been available in large quantities. Similarly, there is no data available for April, May or June in 1939, the only possible estimate being provided by the data from the Esbjerg line, where it crosses the Bremen. In order to make use of this, the annual maxima for this line have been shown for the years 1937–39 in Text-fig. 5, in addition to those for the other three lines (there is no corresponding graph for 1936, since no records were obtained in the spring of that year). These results show an increase in 1939 over 1938 similar on the whole to that on the Rotterdam line ; the apparent decrease in 1938 after 1937 may be misleading owing to the absence of any record in April. The general distribution shows the main areas to be in the east in these years, as in 1932 and 1933 ; 1937 would appear to show an intermediate condition between these years and those with a marked westerly component (1934–1936). The whole series of records seems to show a clear-cut cycle. After being fairly abundant on the two southern lines, Phaeocystis became scarcer on the whole and then even more abundant (at least on the Rotterdam and perhaps on the Esbjerg line) in 1938–39. Whilst limited mainly to the east at first, it extended over to the west and then was limited to the east again. Perhaps we can also make the point that after being insignificant on the Copenhagen line, small but significant quantities were found until, in 1939, it decreased again.

In so far as the Dinoflagellates appeared to increase until 1937 or 1938 and then to decrease to values resembling those of the earlier period, we may point out a possible relation with Phaeocystis. Whilst they are out of phase, it seems that they may be more or less inversely related. In the preceding ‘ Bulletin ’ we pointed out that the diatoms, in turn, had increased more or less progressively throughout the earlier years until 1935, 1936 or 1937 (the various maximal years in most species), after which they were on the whole scarcer, returning during 1938–39 in some cases to values resembling those found in 1932–34. In particular 1939 was a year of very low values for most species.

The flagellate results taken in conjunction with those for the diatoms show quite a striking picture for the southern area. Most of the phytoplankton species had become quite scarce during the spring and summer of 1939 (with the marked exception of Phaeocystis, which became more abundant than usual), so that the area was very thinly populated in comparison with the preceding years. Not only was this shown in the four lines considered above, but also in varying degrees by the southern ends of the lines running up to the north. For these there is no means of comparison with the earlier period, but we see that whilst along their southern lengths the phytoplankton was much scarcer in 1939 than in 1938, towards their northern ends it was either not so much scarcer, or as abundant, or even more abundant. The change becomes more marked as one moves further north. Particularly in the north-east can we note a marked increase in many forms over the previous year; here, again, there is a resemblance between the Dinoflagellates and the diatoms. In the north-west, Phaeocystis (like several other species) also shows a slight increase in 1939, although the quantities here are much smaller than in the south. It is noteworthy that in this feature the two areas are in agreement, whereas they are dissimilar in so many others. Phaeocystis seems to have been insignificant in the north-east in both years. Finally we see that Halosphaera was certainly scarcer in the south in 1939, and perhaps rather more abundant in the north.

General Remarks

The Flagellate data in general provide further evidence of the various points made at the conclusion of the preceding diatom paper. The series of records confirms the general nature of " patchiness," and of rapid numerical change in relatively short time and space intervals (*cf.* for example, Plates XLIV and LXII). Yet the persistence of the two large areas of Dinoflagellate production in the north-west and the south-east provides perhaps even better evidence than in the diatoms of the general agreement between the adjacent and intersecting Recorder lines (*e. g.* Plates XLIV and LXV). Exceptional disagreements are often found to be due to larger time intervals than usual between the neighbouring records. The nature of these two regions is itself a matter of interest. To anticipate a later report (Marshall, in the press), there are signs of a relationship between the distribution of some of the present species in the north-western area and that of *Sagitta elegans elegans* Verril (amongst other forms). Correlations of this type will need to be considered from the biological as well as the physical point of view (*cf.* Lucas, 1938, and, for the Dinoflagellates, Meschkat, 1939), the two being inseparable in practice. At present, however, this relationship seems to point to a possible association between the organisms found in this area and the Atlantic influence which may be exerted there. It seems noteworthy that much of the diatom and flagellate data presented in the preceding and present papers conforms to the general and " admittedly idealized " picture of the " North Sea Area as a whole " drawn by Russell (1939). The detailed agreements and disagreements will be discussed at a later stage, but we may note that this north-western area corresponds broadly to that characterized as "*elegans* water," whereas the south-eastern area corresponds to his area of " coastal water." Jörgensen (1911*b*) had made several references to the probable additions to the North Sea stocks of some of the species through periodical invasions from the outer ocean, mainly *via* the north-west. In this connection reference to ' Bulletin ' No. 10 (Lucas, Marshall and Rees, 1942) shows that, on a Recorder line between Pentland and Faeroe Bank, *Ceratium fusus* and *C. lineatum* were the only abundant forms in 1939, *C. fusus* being much sparser than in the neighbouring North Sea. *C. macroceros* and *C. longipes* were remarkably scarce there at the depth sampled. This cannot be discussed further here, but we may point out that the Ceratia present a graded series regarding their overall distribution in relation to the two entrances to the North Sea (see Plates XL to LXII). *C. lineatum* had its highest numbers limited to the north-west in both years. *C. tripos* extended more towards the centre in 1938, as did *C. macroceros*, the latter, along with *C. horridum*, having secondary maximal areas in the south-east in both years. Whilst *C. furca* was mainly limited to the northern half in 1939, it also had a smaller south-eastern maximum in 1938 and, as we have seen, *C. fusus* was very abundant in both regions in both years, although attaining rather higher numbers in the north-west. The contrast between these and *C. longipes* is considerable, since this showed only a south-eastern maximal area in 1938 and a north-eastern one in 1939. In association with the last point, some of the other forms were more abundant in the north-east in 1939 than in 1938, whilst all, even *C. fusus*, were much scarcer in the south. These matters may be taken in conjunction with several features regarding the diatoms which we tentatively associated with signs of an *increased* flow of (possibly phosphate-scarce) water into this area from the English Channel after the early months of 1938 (Lucas, 1941, p. 44). The Dinoflagellates provide more evidence suggesting that the phytoplankton-productive water of the preceding years may have moved out of the area in a northerly or north-easterly direction (*vide* some of the species which were more abundant in the north-east in 1939, such as *C. longipes*, and some, such as the Dinophysidae, showing signs of an east to west trend then). Jörgensen has mentioned that *C. fusus*, for example, may be brought into the North Sea *via* the Dover Straits, but it is also possible that such organisms may be *pushed out* by the incoming water, just as in other years they may be carried into the southern area from the north in association with water which is tending to move from the North Sea into the Channel. However this may be, the flagellate data provide confirmatory evidence on the whole for the cycle of changes since 1932, which were first deduced from the diatom records up to 1937 (Lucas, 1940), extended up to 1939 (Lucas, 1941), and have already received some confirmation from zooplankton records for the earlier period (*cf.* Rae and Fraser, 1941).

SUMMARY.

1. Comparable data to that for the diatoms in ‘ Bulletin ’ No. 8 (Lucas, 1941) are shown here for various flagellates in the North Sea during 1938 and 1939. Changes in composition and distribution of the Dinoflagellate species are shown in Plates XL to LXII. Those for Phaeocystis appear in Plate XXXIX and those for *Halosphaera viridis* in Text-fig. 6.
2. The main features of the distribution of the whole group of Dinoflagellates

is reviewed on pp. 48 to 55, that of the individual species, etc., on pp. 57 to 63, and of other flagellates on pp. 63 to 65.

3. Comparisons are made between the present data for the southern area and those of 1932–37. After increasing variously until 1937 or 1938 the Dinoflagellates were all found to be much scarcer in 1938 and/or 1939. Phaeocystis, on the other hand, was scarcer from 1934 until 1937, but increased again during 1938 and 1939.

4. Other changes, in association with those above, present together a cycle of events which sufficiently resembles those seen in the diatoms to appear confirmatory (pp. 65 to 68). In conjunction, some remarks are made on possible relations between these features and the hydrography of the area (p. 68).

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EXPLANATION OF PLATES XXXIX TO LXII.

PLATE XXXIX.

Charts showing the distribution of the major patches of Phaeocystis during 1938 and 1939. For the data in other months see p. 63. Symbols are used to denote the varying quantities in c.c. per mile on each ten-mile block (see scale). Where more than one record has been obtained in any month, they have been shown " in parallel " (the earlier one above) and bracketed together.

PLATES XL–XLII.

Charts showing the distribution of *Ceratium furca* (p. 57) month by month from January, 1938, to June, 1939. Numerals and symbols are used to denote the varying numbers per mile on each ten-mile block (for scale see inset). Where more than one record has been obtained in any month, they have usually been shown " in parallel " (the earlier one above) and bracketed together. Where this has not been possible, one representative record has been shown in the usual manner and the other(s) have been shown in the margin (as in August and November, 1938), the symbols I–III denoting the order of the series (for dates see 'Bulletin' No. 8). The data for July and August, 1939, are shown in Plate LI.

PLATE XLIII.

Charts showing the distribution of the major patches of *Ceratium lineatum* (etc.) during 1938 and 1939. For the data in other months see p. 61. (See also explanation of Plates XL–XLII above).

PLATES XLIV–XLVI.

Charts showing the distribution of *Ceratium fusus* (p. 58) month by month from January, 1938, to June, 1939, arranged in the same manner as those of *C. furca* (see explanation of Plates XL–XLII above.) The data for July and August, 1939, are shown in Plate LI.

PLATE XLVII.

Charts showing the distribution of the major patches of Peridinium (spp., etc.) during 1938 and 1939. For the data in other months see p. 62. (See also explanation of Plates XL–XLII above.)

PLATES XLVIII–L.

Charts showing the distribution of *Ceratium tripos* (p. 59) month by month from January, 1938, to June, 1939, arranged in the same manner as those of *C. furca* (see explanation of Plates XL–XLII above). The data for July and August, 1939, are shown in Plate LI.

PLATE LI.

Charts continuing the data for *Ceratium furca, fusus* and *tripos* into July and August, 1939, but otherwise arranged as in Plates XL–XLII (see explanation).

PLATES LII–LIV.

Charts showing the distribution of *Ceratium macroceros* (p. 60) month by month from January, 1938, to June, 1939, arranged in the same manner as those of *C. furca* (see explanation of Plates XL–XLII above). The data for July and August, 1939, are shown in Plate LIX.

PLATE LV.

Charts showing the distribution of the major patches of Dinophysis spp. during 1938 and 1939. For the data in other months see p. 62. (See also explanation of Plates XL–XLII above.)

PLATES LVI–LVIII.

Charts showing the distribution of *Ceratium horridum* (p. 60) month by month from January, 1938, to June, 1939, arranged in the same manner as those of *C. furca* (see explanation of Plates XL–XLII above). The data for July and August, 1939, are shown in Plate LIX. In the chart for July, 1938 (Plate LVII), the lithographic process has failed slightly in some copies at the north-west corner ; the penultimate value on line A1 should be 6 (= 600).

PLATE LIX.

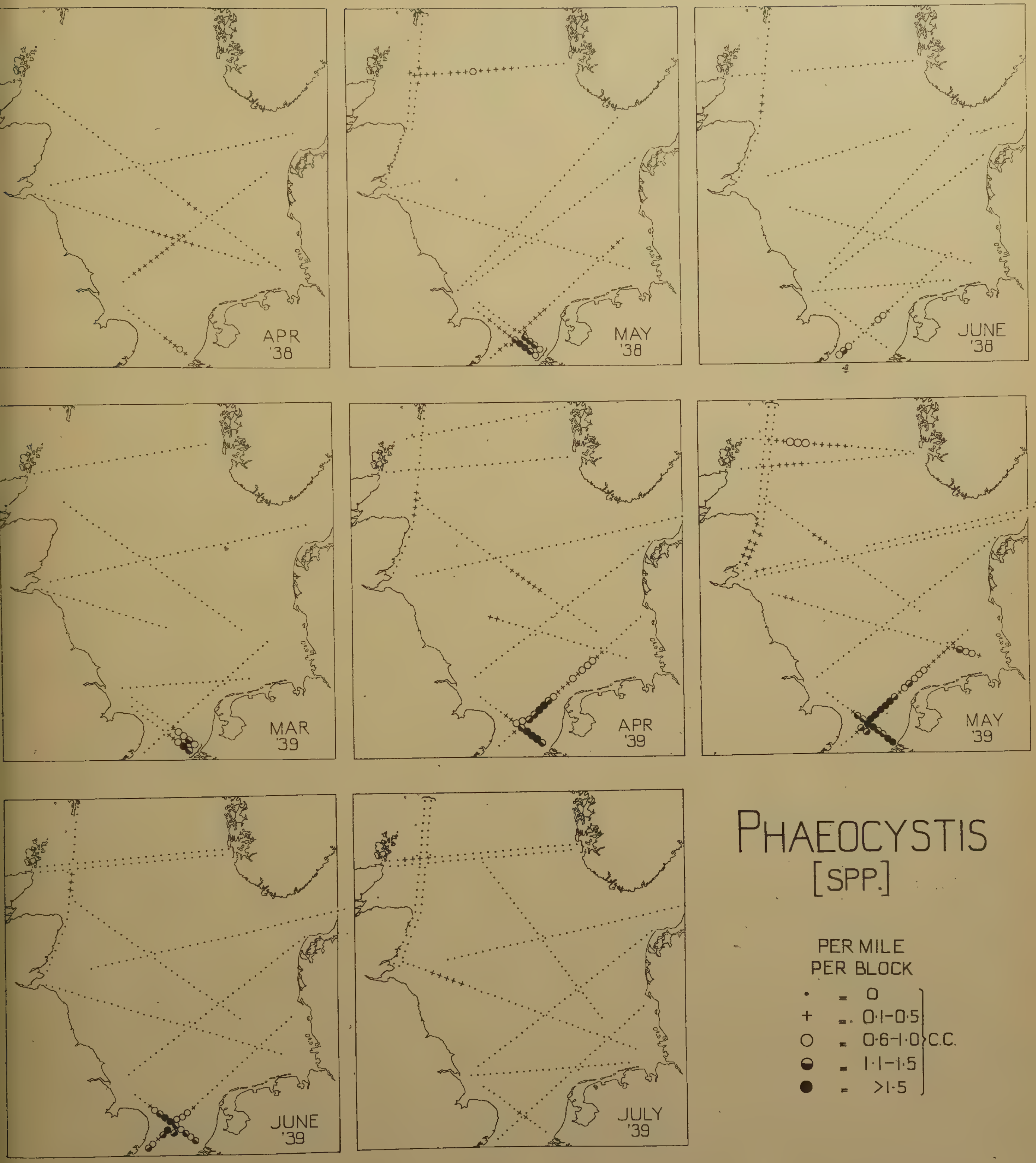
Charts continuing the data for *Ceratium macroceros*, *horridum* and *longipes* into July and August, 1939, but otherwise arranged as in Plates XL–XLII (see explanation).

PLATES LX–LXII.

Charts showing the distribution of *Ceratium longipes* (p. 61) month by month from January 1938, to June, 1939, arranged in the same manner as those of *C. furca* (see explanation of Plates XL–XLII above). The data for July and August, 1939, are shown in Plate LIX.

Corrigendum.

As the result of an oversight the data for the Pentland-Bergen record of October 22, 1938, has been slightly misplotted on each occasion on which it has been used. Instead of being in the direct line, as in the previous record, the direction was changed during the voyage, the true route being as in Plate III of ‘ Bulletin ’ No. 7. For most purposes the error may be regarded as a slight one.

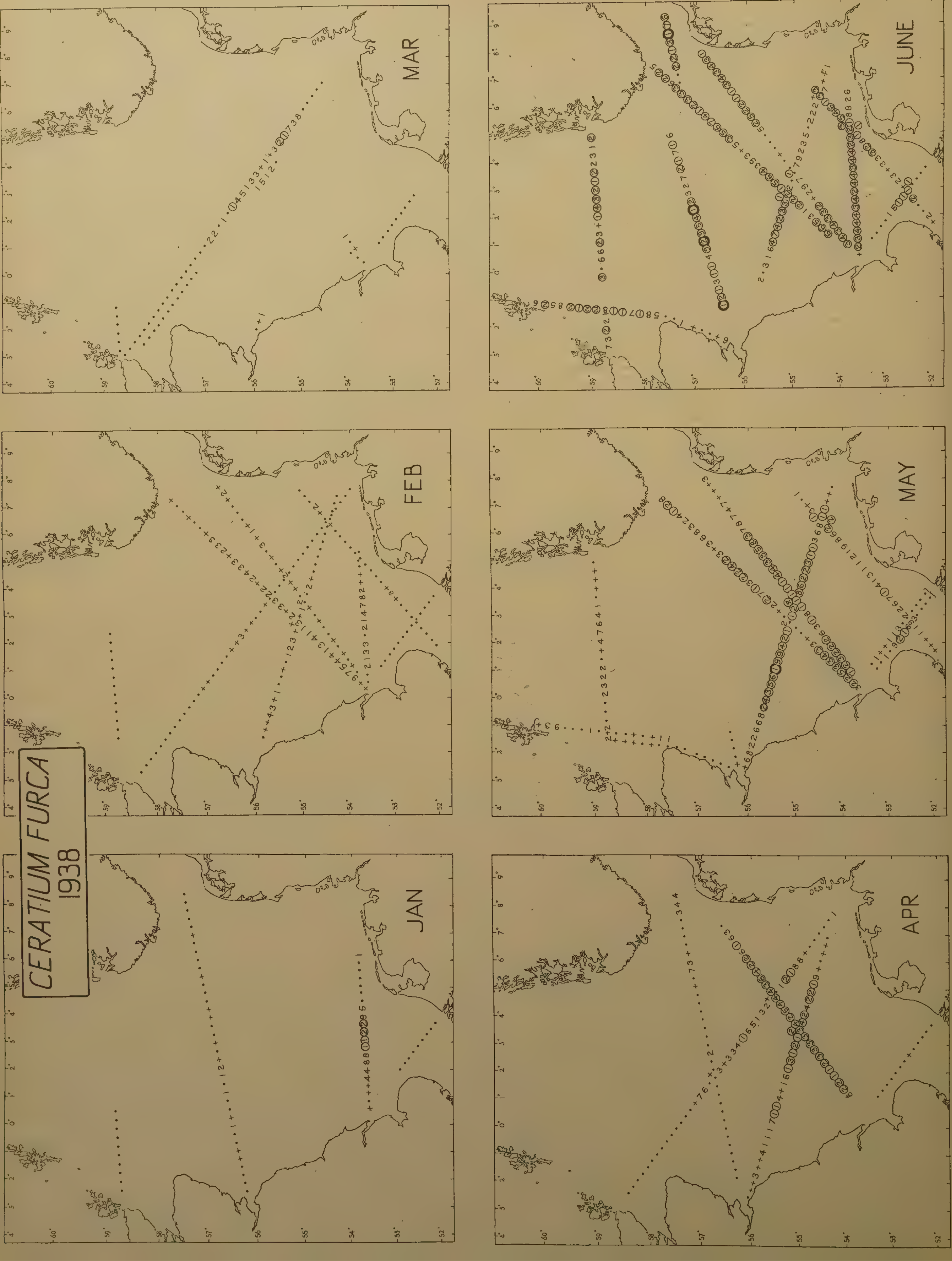

APR '38
MAY '38
JUNE '38
MAR '39
APR '39
MAY '39
JUNE '39
JULY '39

PHAEOCYSTIS [SPP.]

PER MILE
PER BLOCK

• = 0
+ = 0·1–0·5
○ = 0·6–1·0 C.C.
◒ = 1·1–1·5
● = >1·5

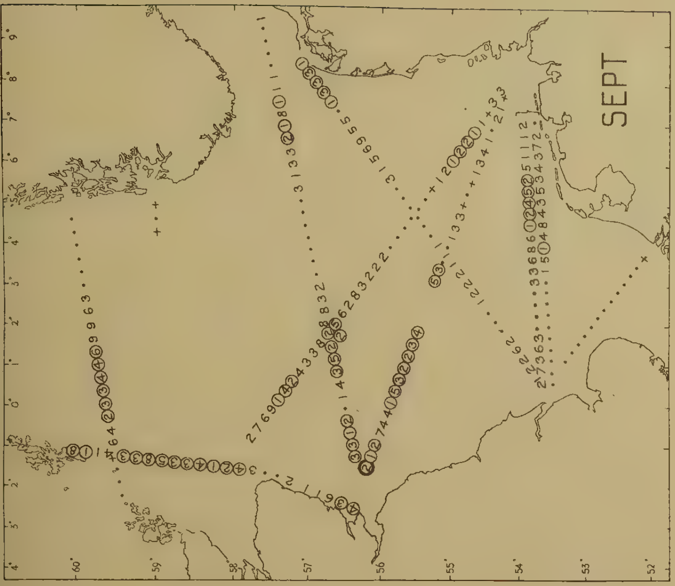
PLATE XL

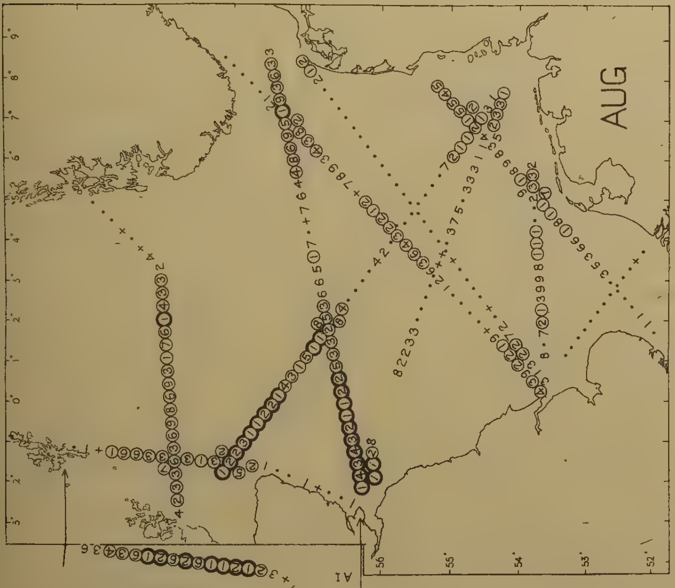


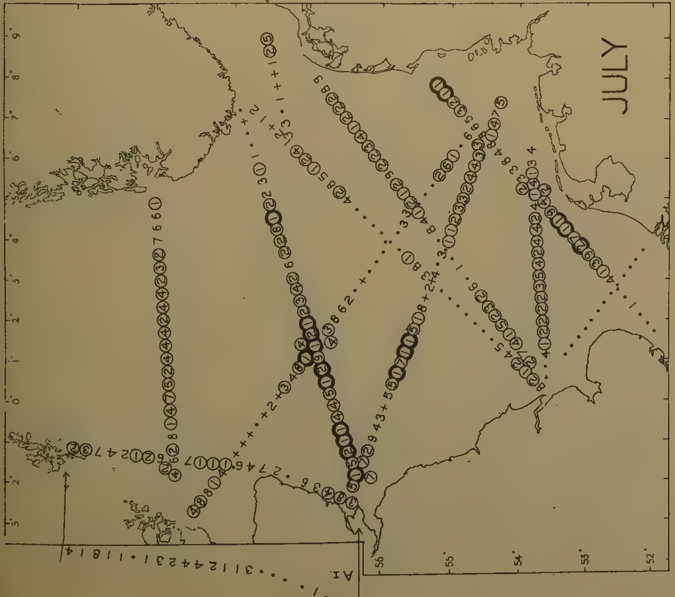
JAN
FEB
MAR
APR
MAY
JUNE

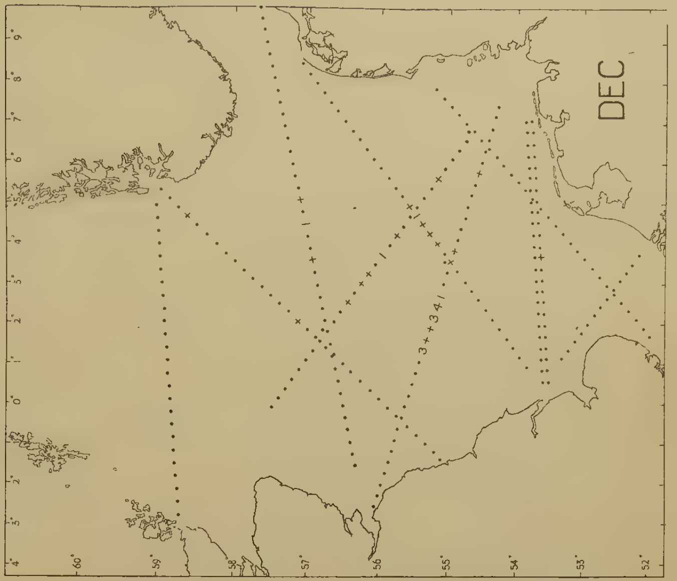
CERATIUM FURCA
1938

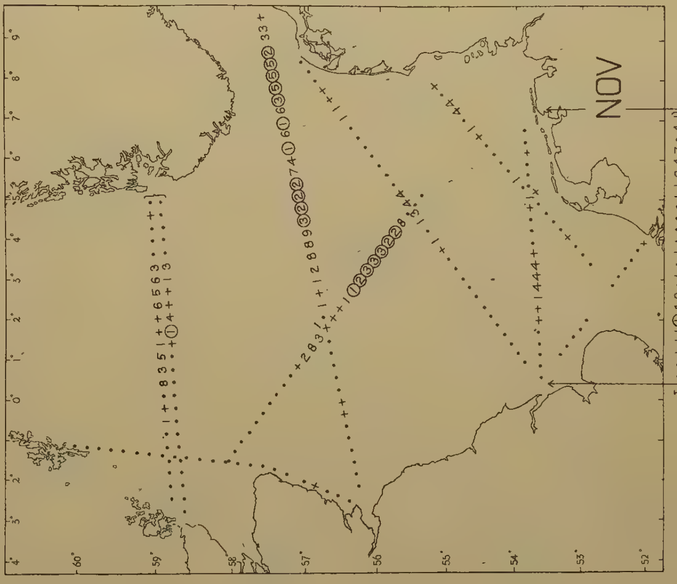
PLATE XLI


SEPT


AUG
A1.


JULY
A1.


DEC


NOV

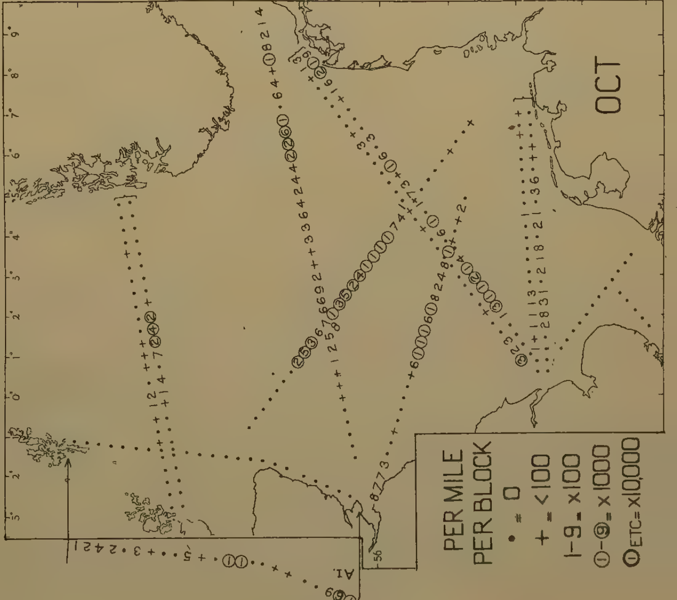
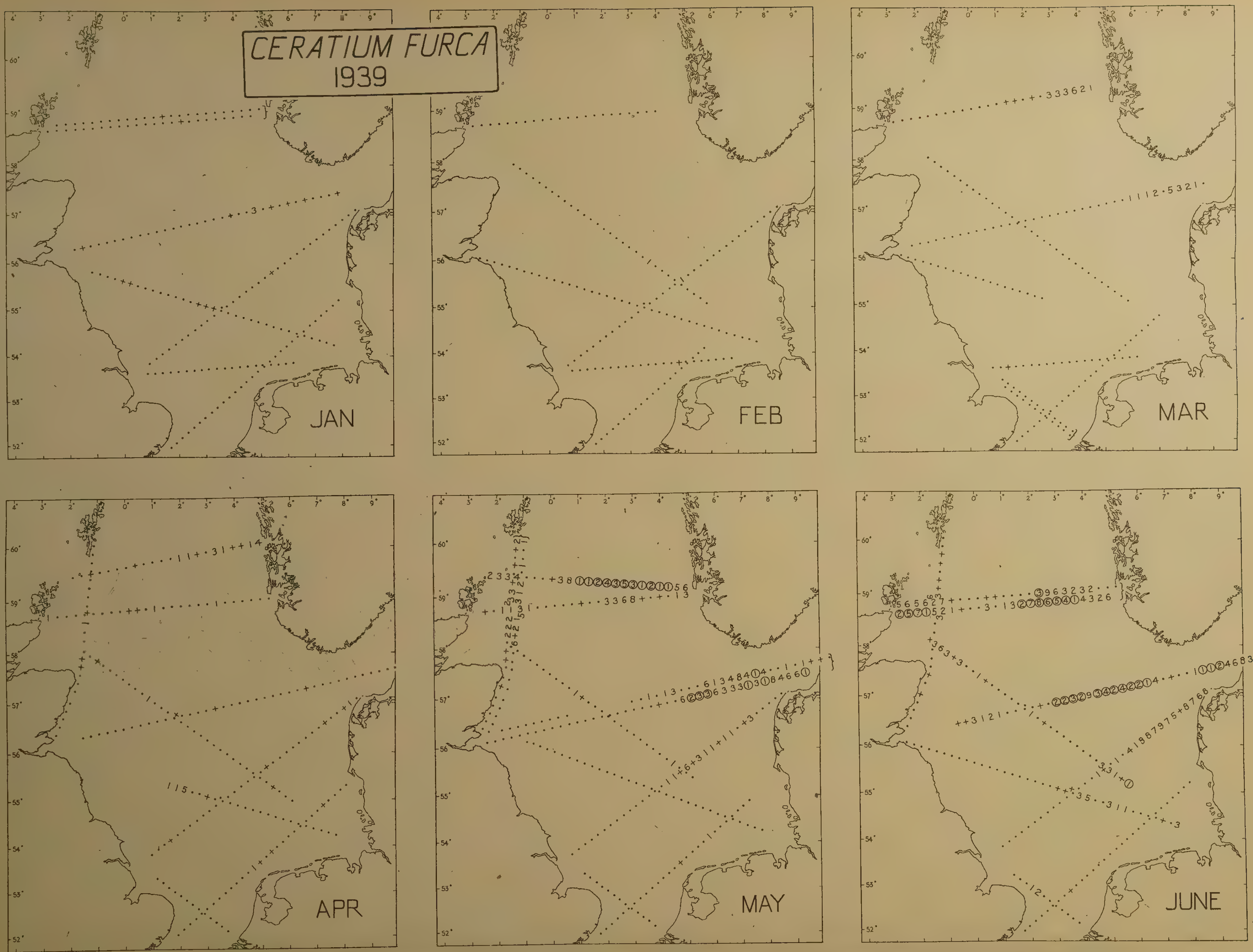

OCT
A1.
PER MILE
PER BLOCK
• = 0
+ = <100
1-9 = x100
①-⑨ = x1000
①ETC = x10000

PLATE XLII



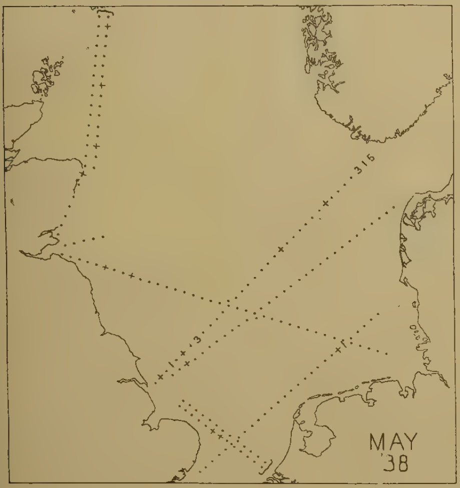
CERATIUM FURCA
1939

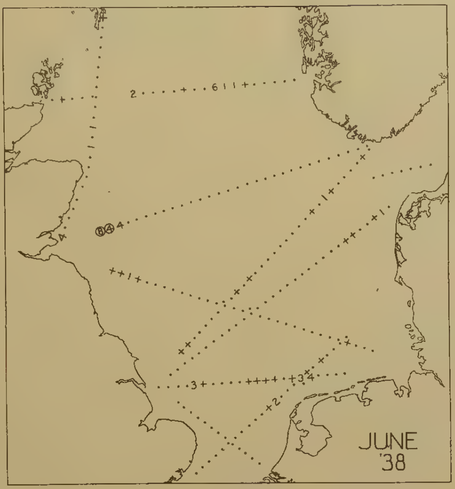
JAN
FEB
MAR
APR
MAY
JUNE

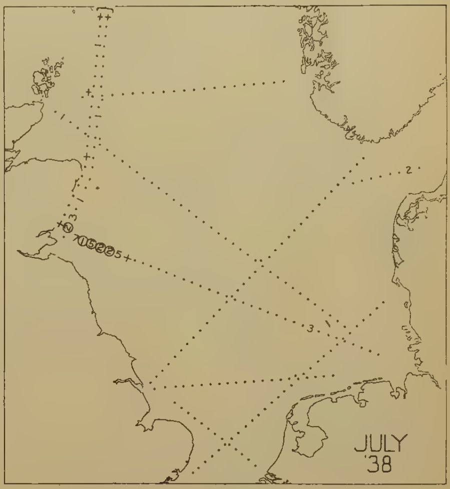
CERATIUM LINEATUM [ETC]

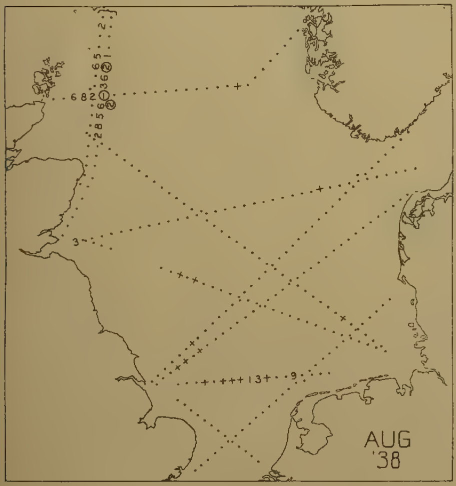
• = 0
+ = <100
1 - 9 = x100
① - ⑨ = x1,000
⓵ ETC. = x10,000

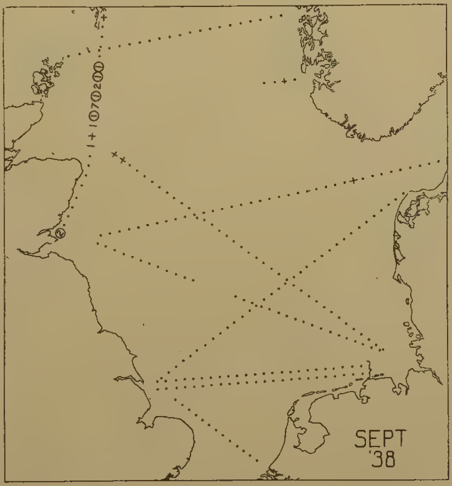
PER MILE
PER BLOCK

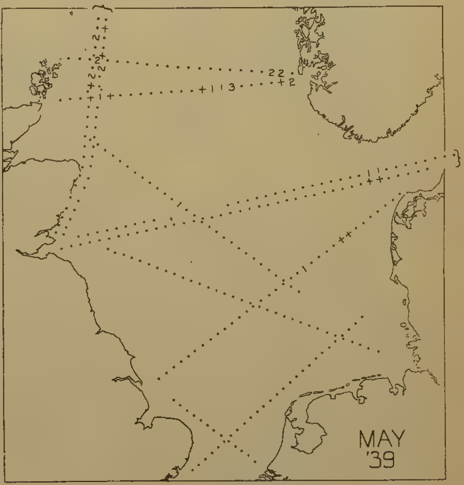


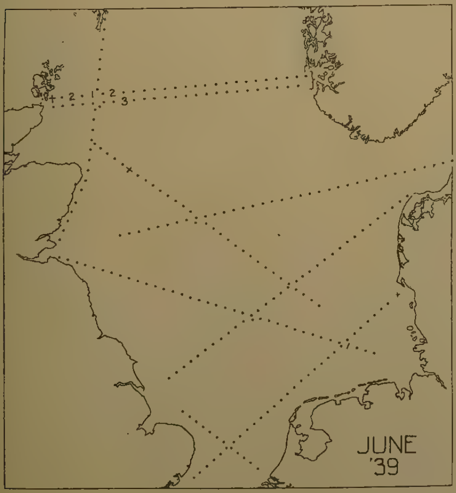


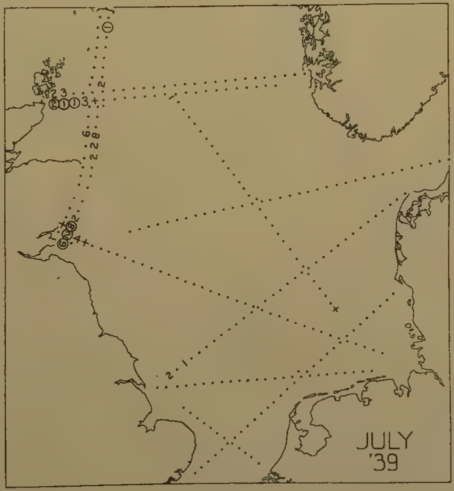












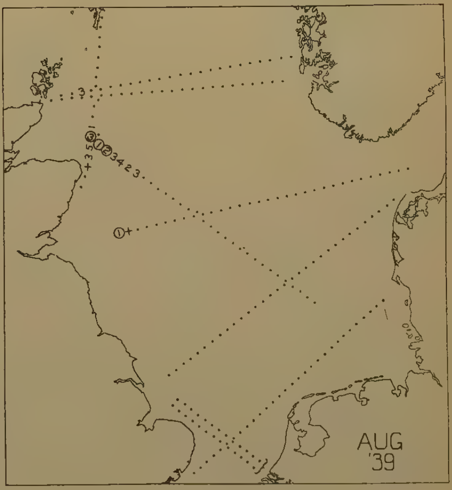
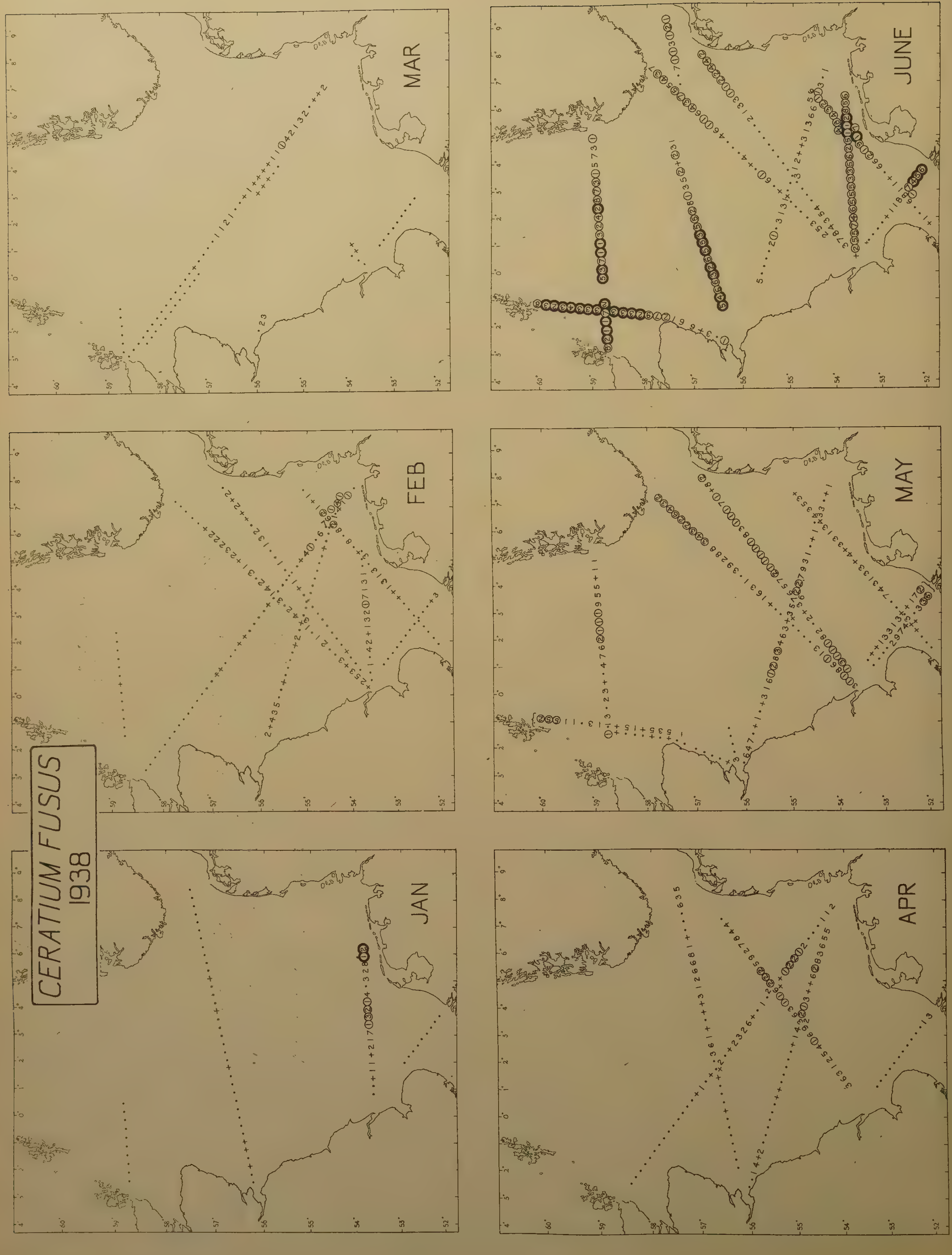


PLATE XLIV


JAN
FEB
MAR
APR
MAY
JUNE

CERATIUM FUSUS
1938

PLATE XLV

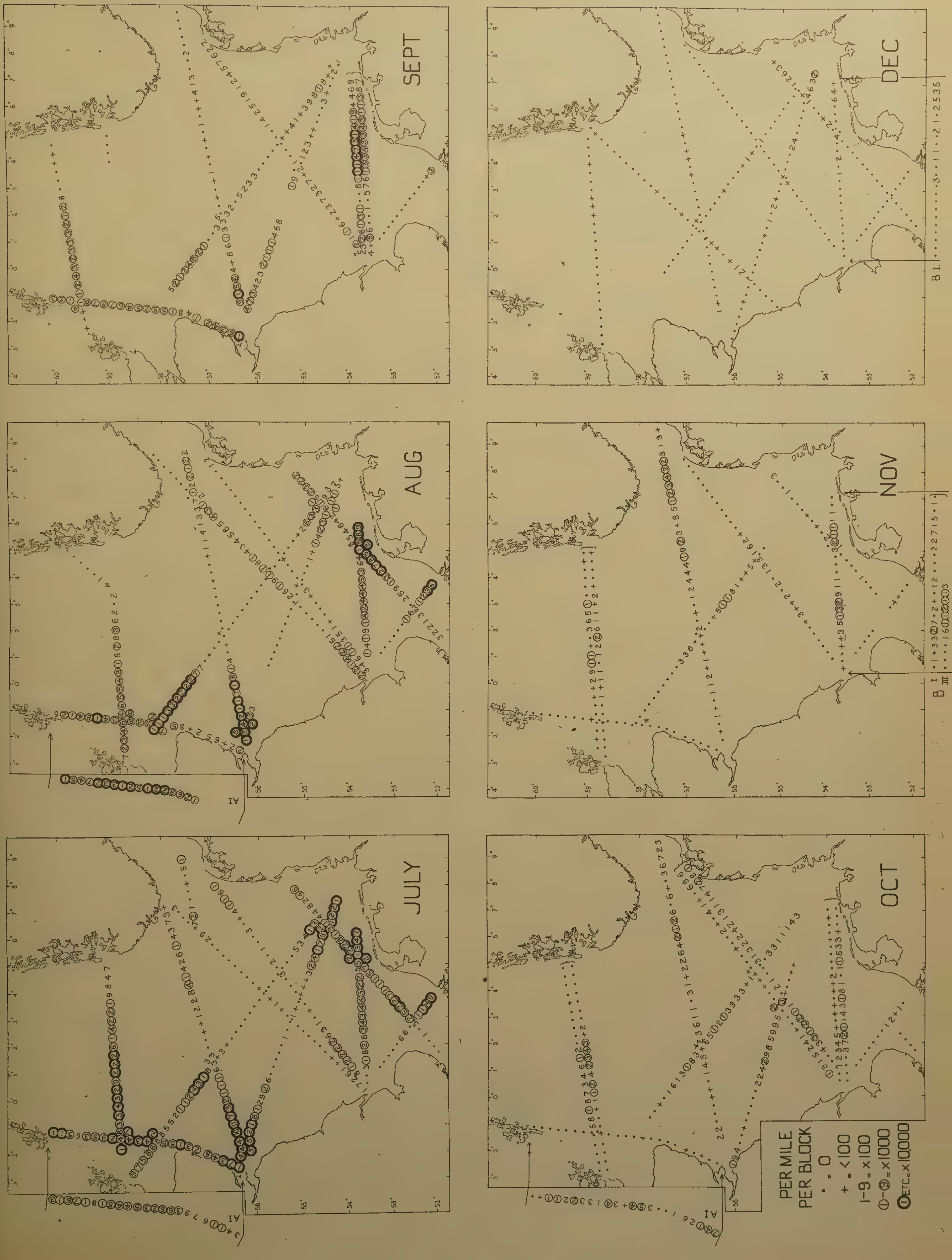
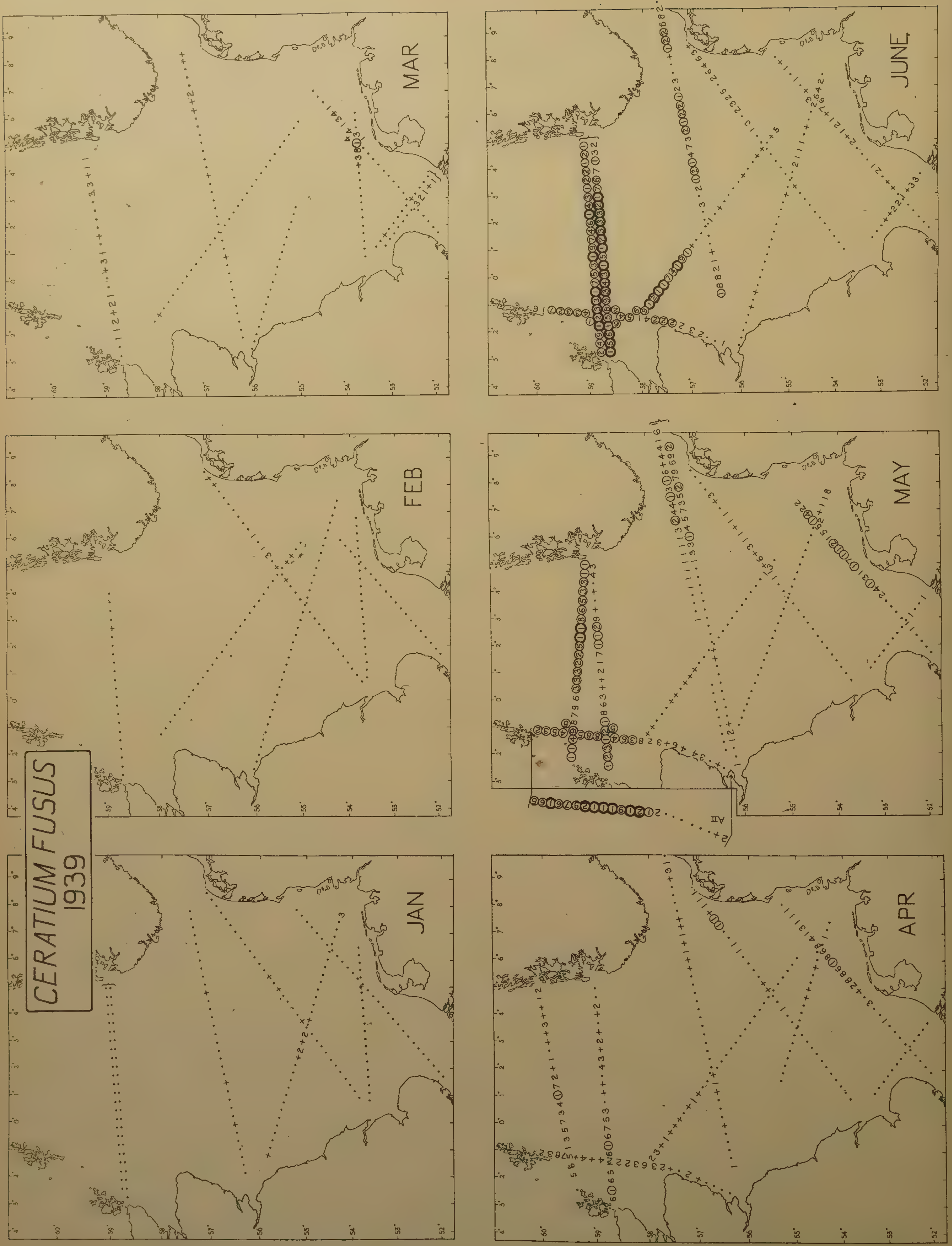

JULY
AUG
SEPT
OCT
NOV
DEC
AI
BI
BIII
PER MILE
PER BLOCK
• = 0
+ = <100
1-9 = x100
①-⑨ = x1000
● ETC = x10,000

PLATE XLVI



CERATIUM FUSUS 1939

JAN
FEB
MAR
APR
MAY
JUNE

PERIDINIUM
[SPP., ETC.]

· - 0
+ - <100
①-⑨ - x100
①-⑨ - x1000
①ETC - x10,000

PER MILE
PER BLOCK

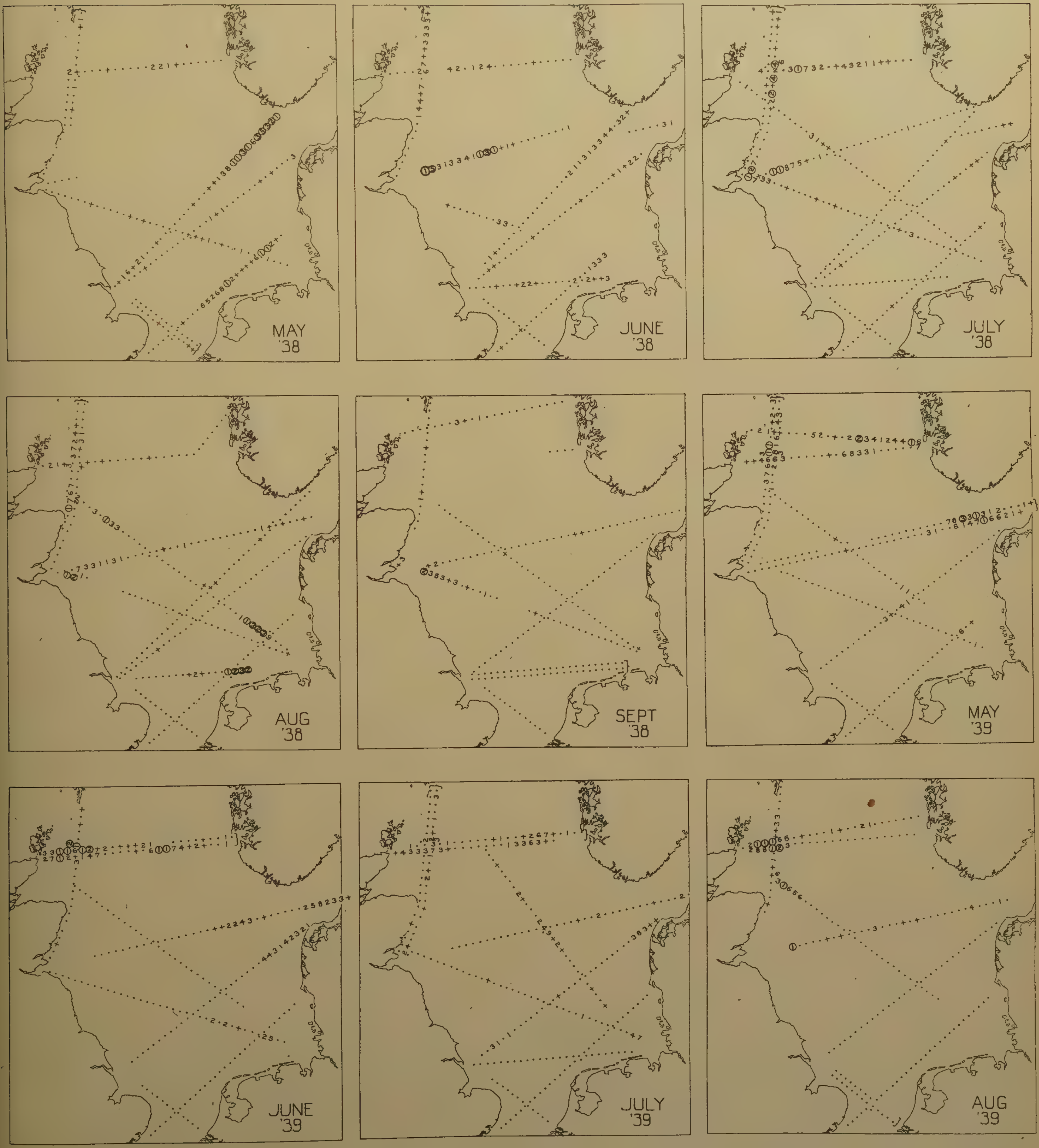
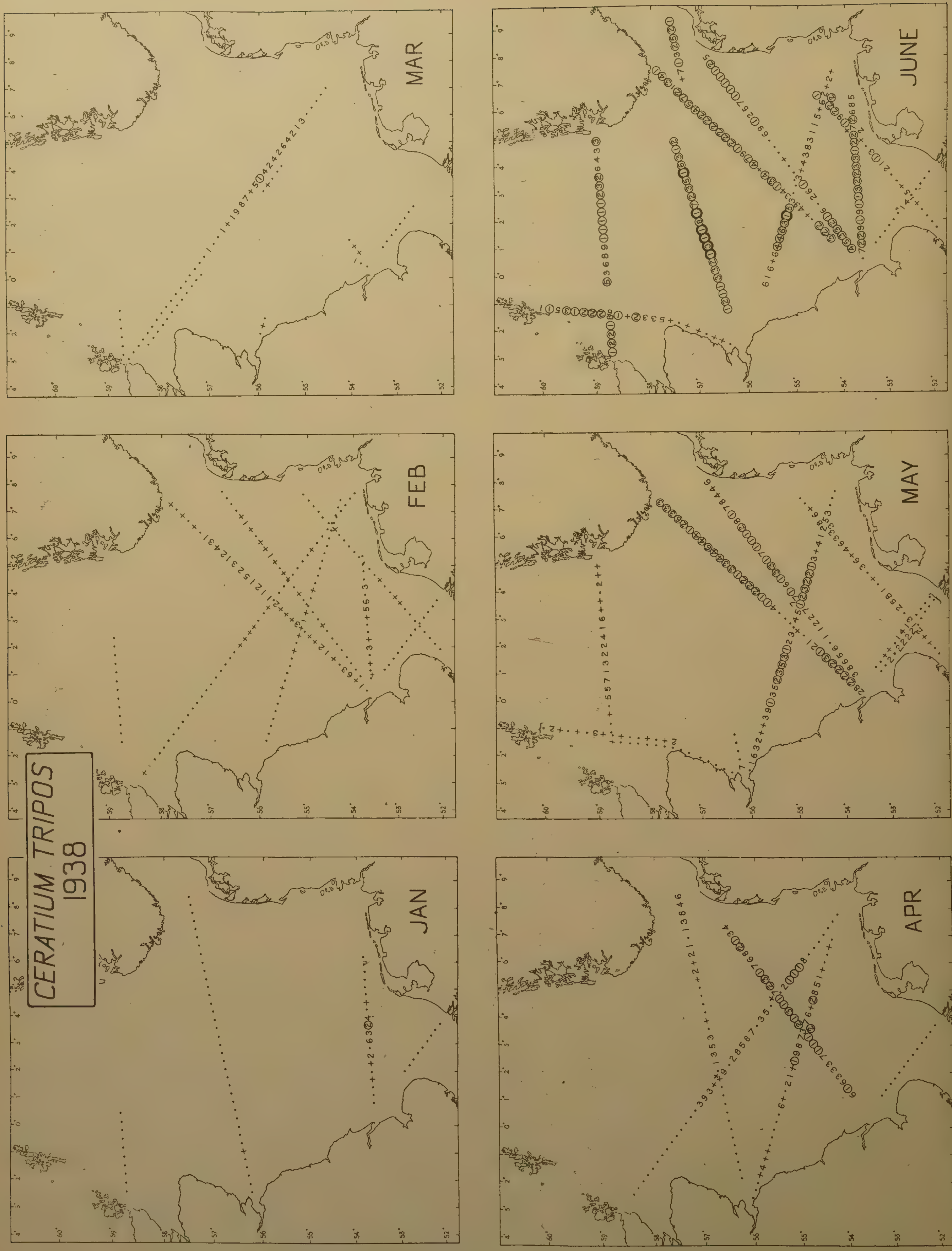

MAY '38
JUNE '38
JULY '38
AUG '38
SEPT '38
MAY '39
JUNE '39
JULY '39
AUG '39

PLATE XLVIII



CERATIUM TRIPOS 1938

JAN
FEB
MAR
APR
MAY
JUNE
60°
59°
58°
57°
56°
55°
54°
53°
52°

PLATE XLIX

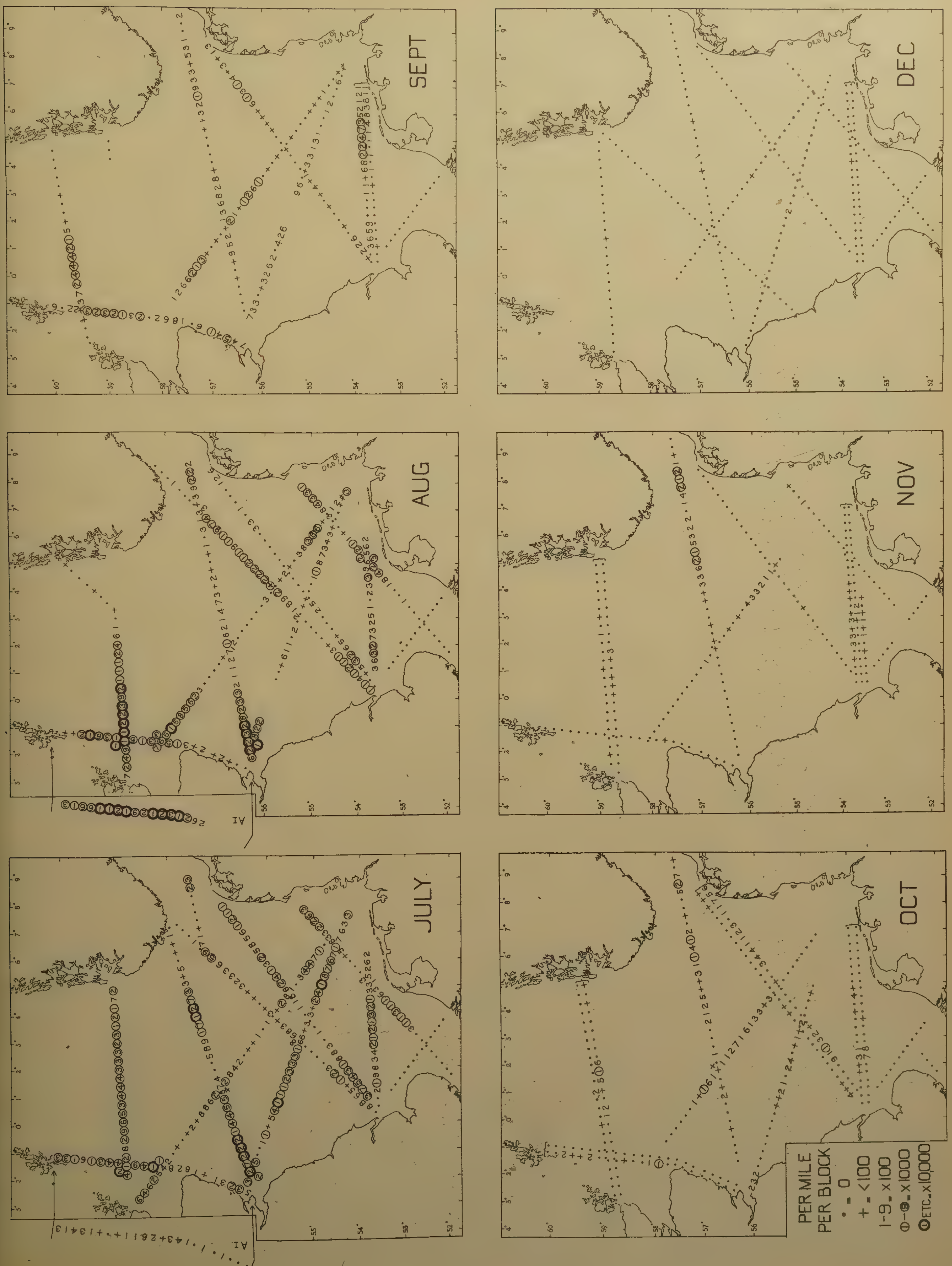
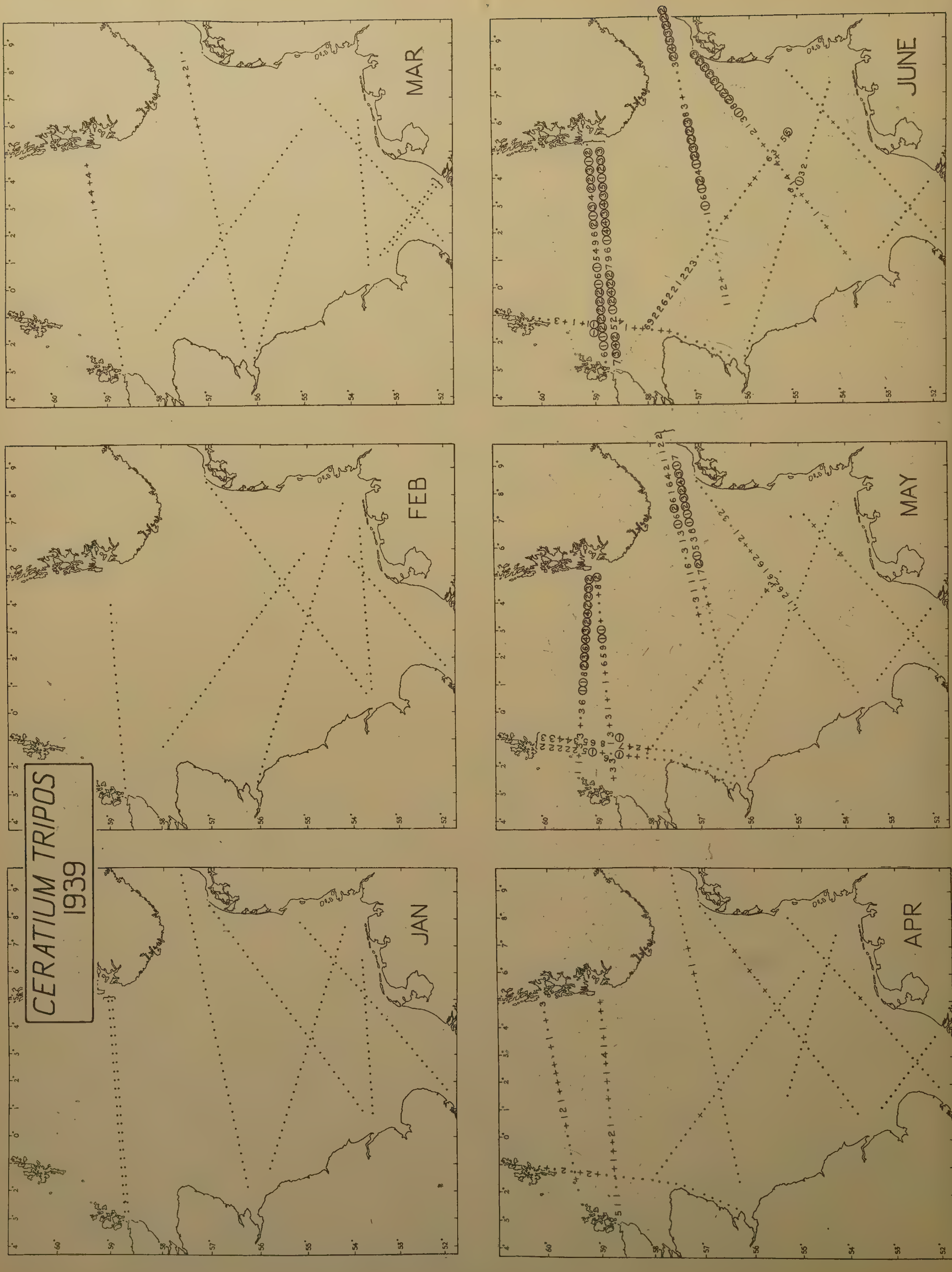

SEPT
AUG
JULY
DEC
NOV
OCT
A1.
A1.
PER MILE
PER BLOCK
• _ 0
+ _ <100
1-9 _ x100
①-⑨ _ x1000
① ETC _ x10,000
60°
59°
58°
57°
56°
55°
54°
53°
52°

PLATE L



CERATIUM TRIPOS
1939

JAN
FEB
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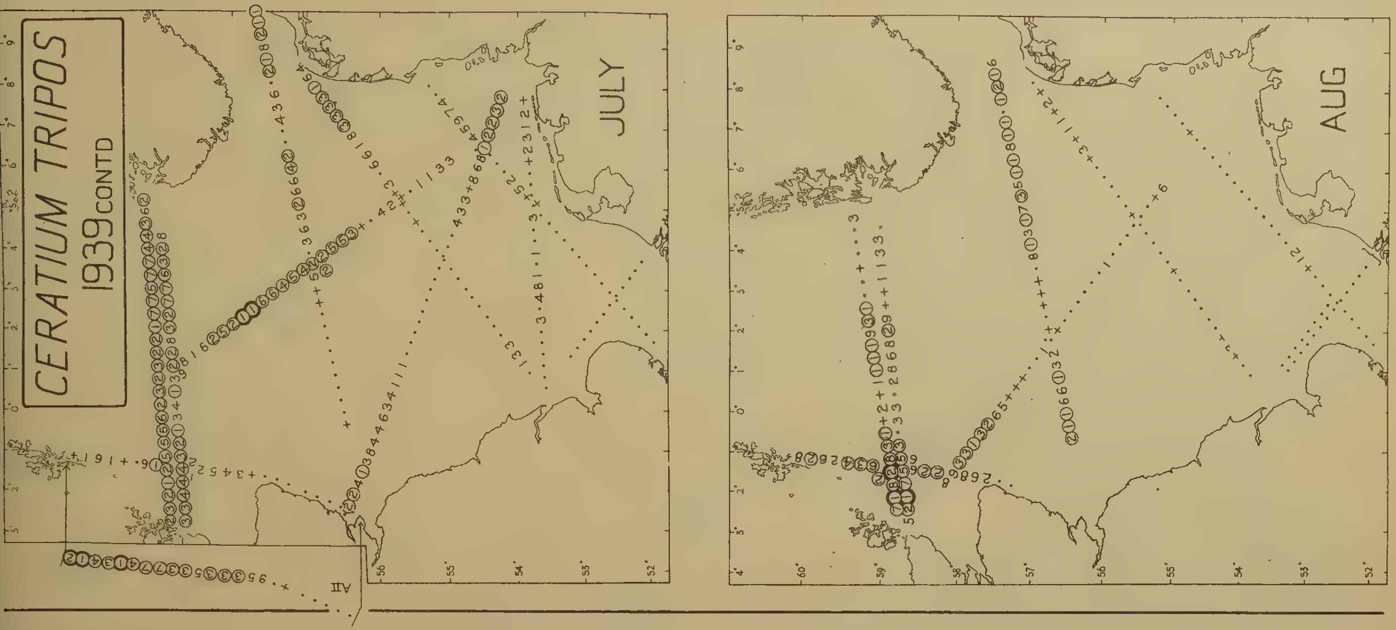
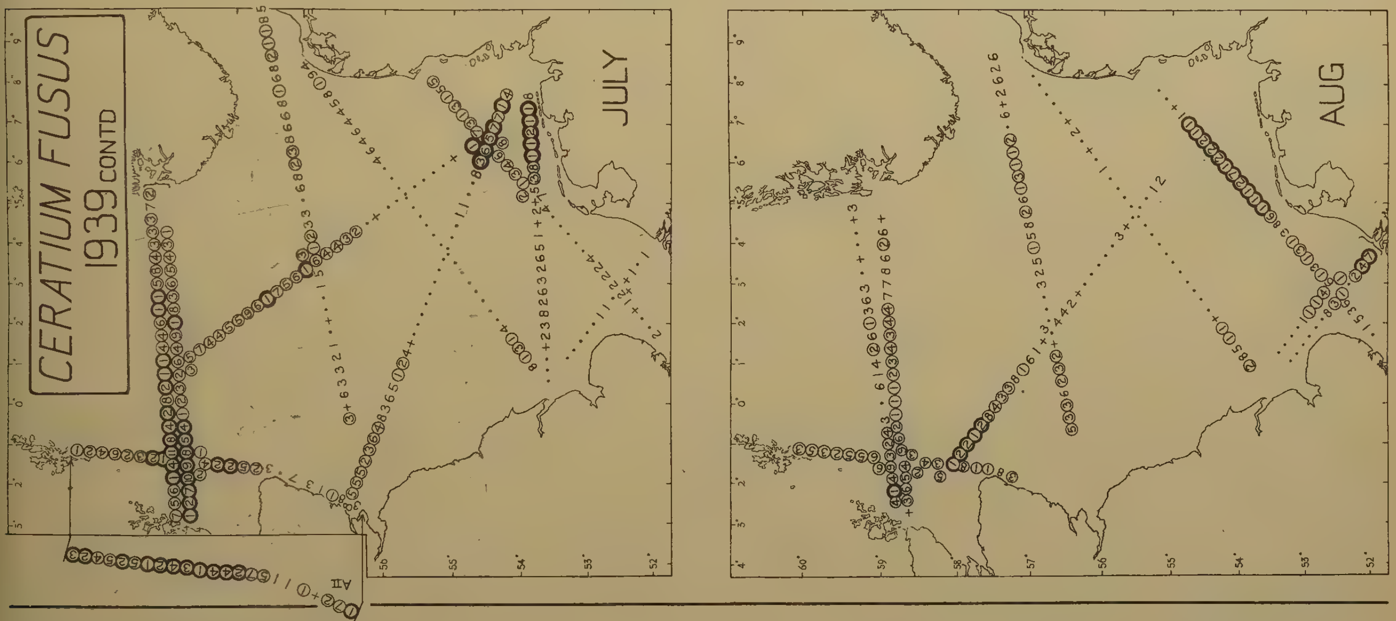
APR
MAY
JUNE


CERATIUM TRIPOS
1939 CONTD
JULY
AUG
A II


CERATIUM FUSUS
1939 CONTD
JULY
AUG
A II

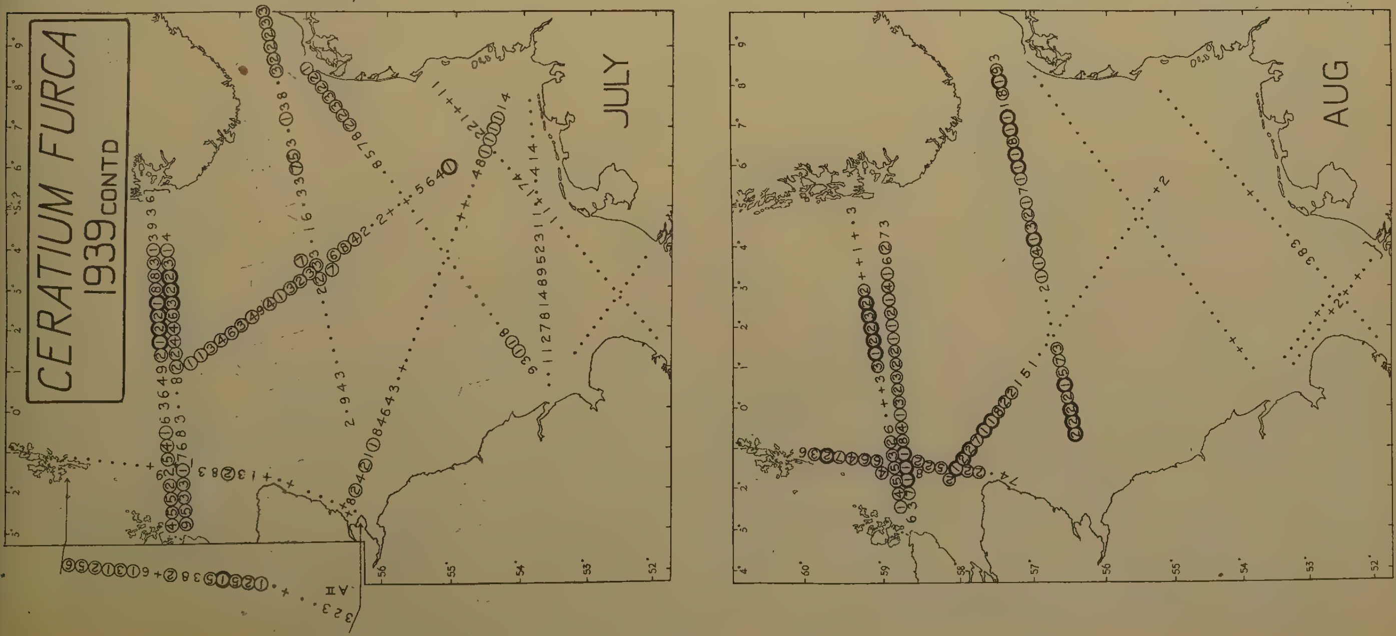
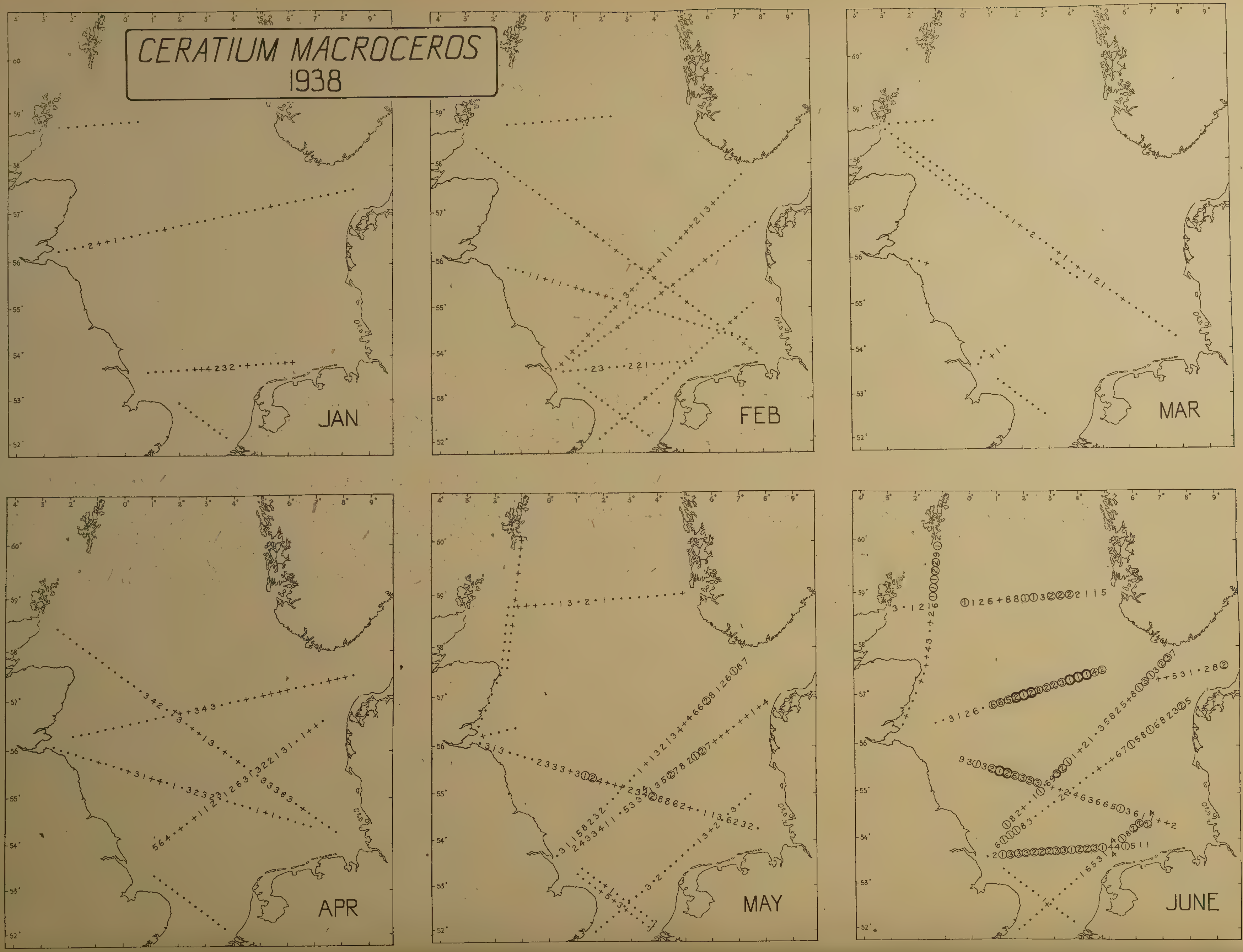

CERATIUM FURCA
1939 CONTD
JULY
AUG
A II

PLATE LII



CERATIUM MACROCEROS
1938

JAN
FEB
MAR
APR
MAY
JUNE

PLATE LIII

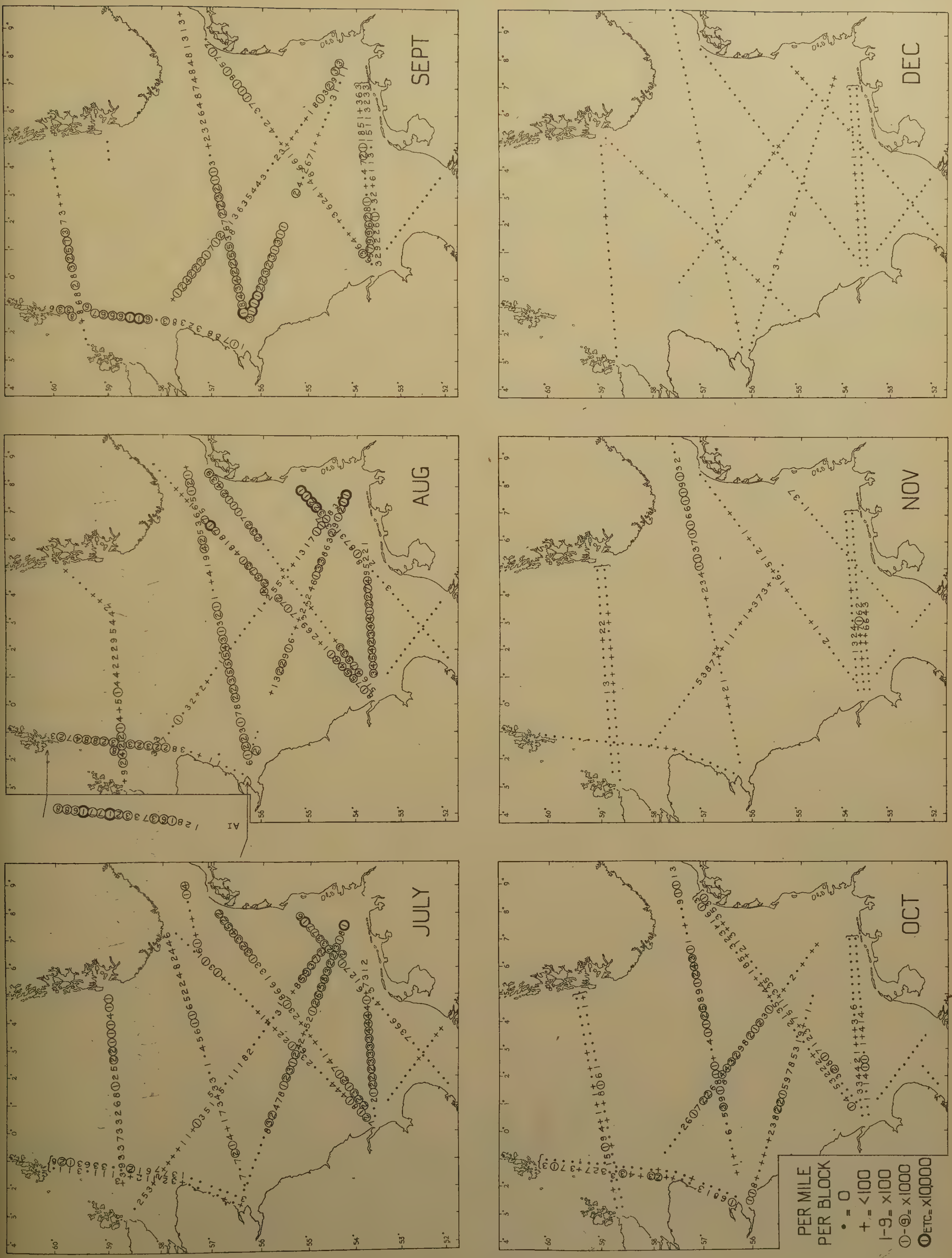
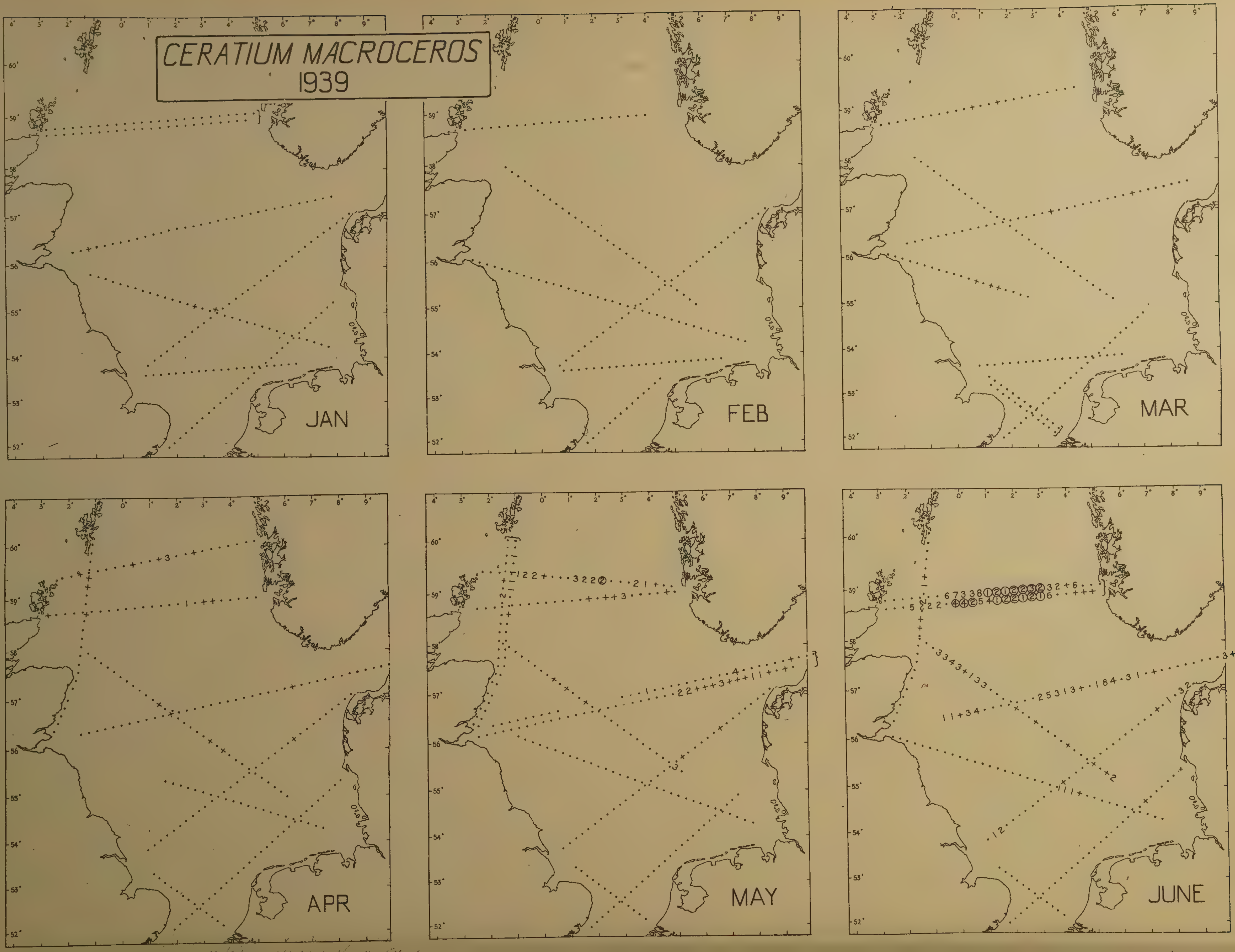

SEPT
DEC
AUG
NOV
JULY
OCT
AI
PER MILE
PER BLOCK
• = 0
+ = <100
1-9 = x100
①-⑨ = x1000
⊕ETC = x10000
60°
59°
58°
57°
56°
55°
54°
53°
52°

PLATE LIV


CERATIUM MACROCEROS
1939

JAN
FEB
MAR
APR
MAY
JUNE

DINOPHYSIS
[SPP.]

• - 0
+ - <100
1-9 - x 100
①-⑨ - x 1,000
① ETC. - x 10,000

PER MILE
PER BLOCK

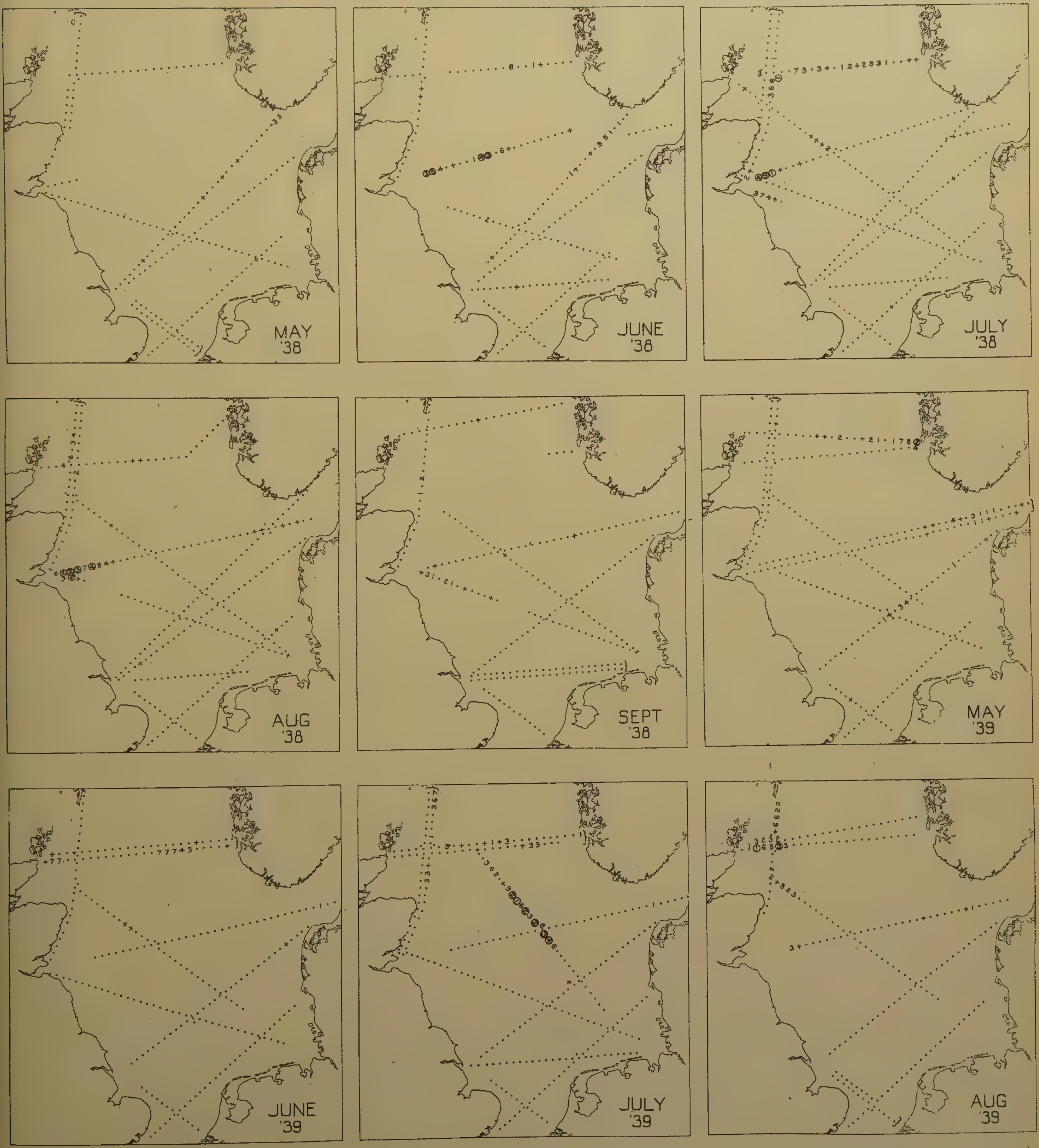
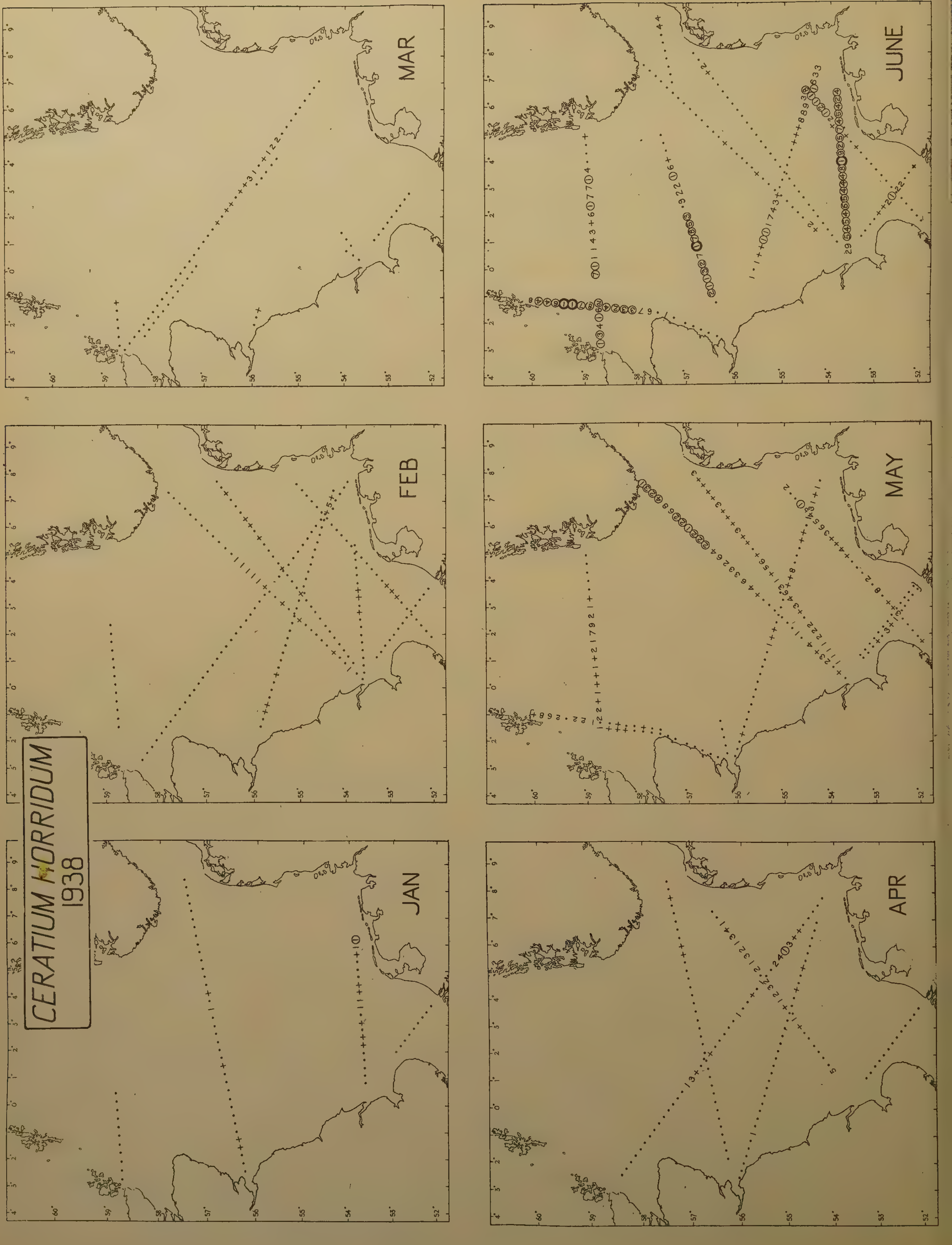

MAY '38
JUNE '38
JULY '38
AUG '38
SEPT '38
MAY '39
JUNE '39
JULY '39
AUG '39

PLATE LVI



CERATIUM HORRIDUM
1938

JAN
FEB
MAR
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MAY
JUNE
60°
59°
58°
57°
56°
55°
54°
53°
52°

PLATE LVII

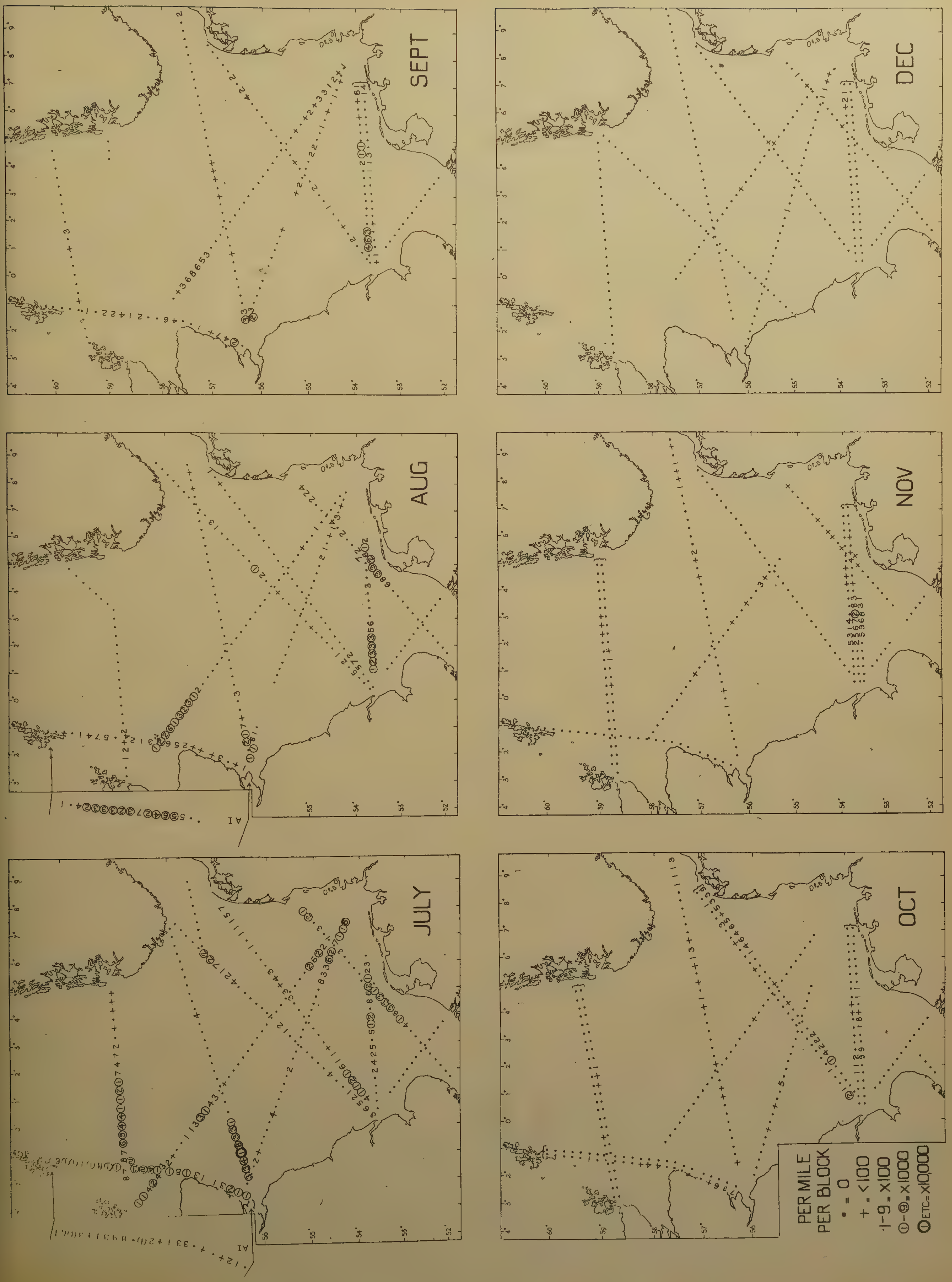
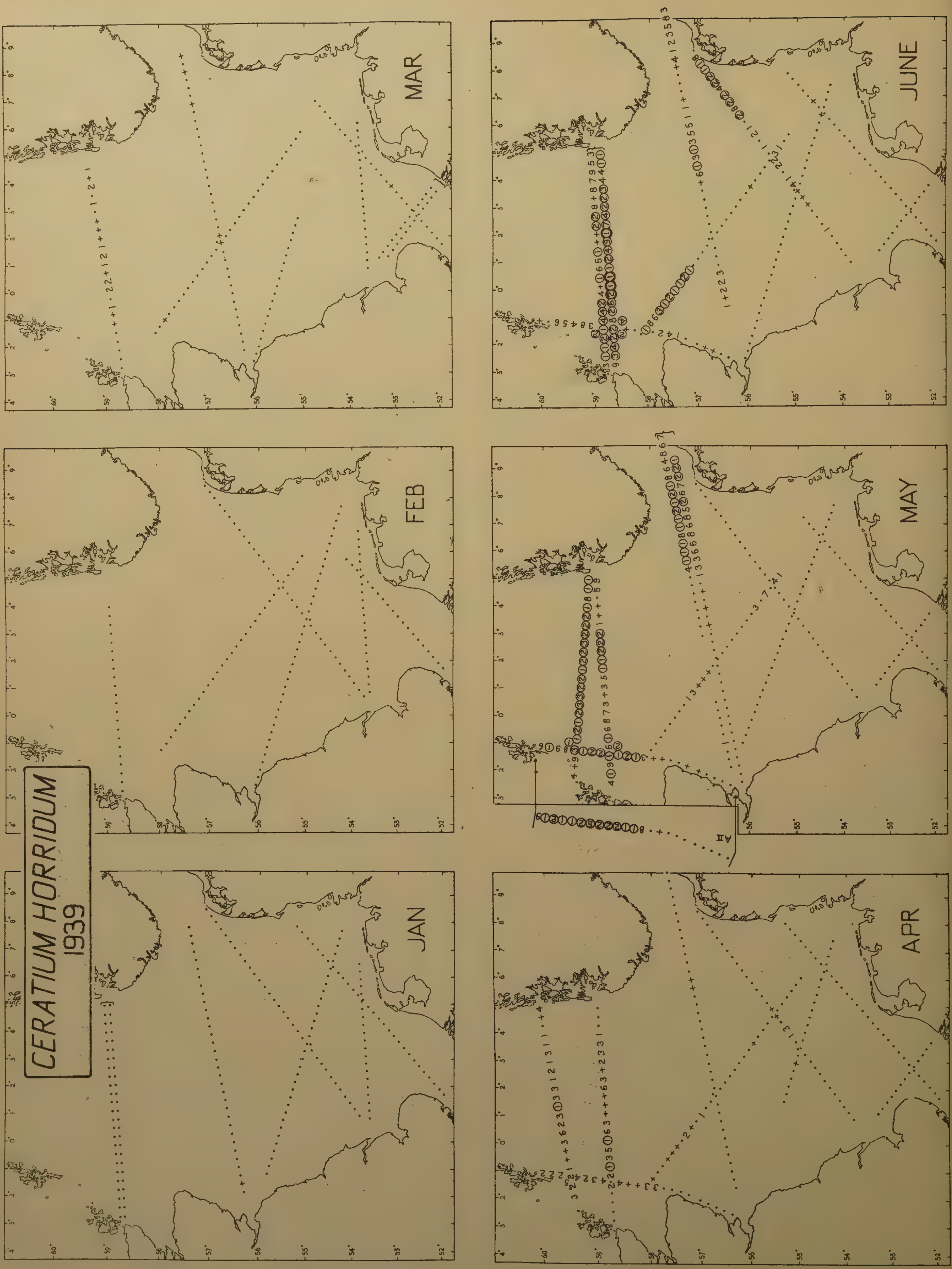

SEPT
DEC
AUG
NOV
JULY
OCT
AI
PER MILE
PER BLOCK
• = 0
+ = <100
1-9 = x100
①-⑨ = x1000
① ETC = x10,000

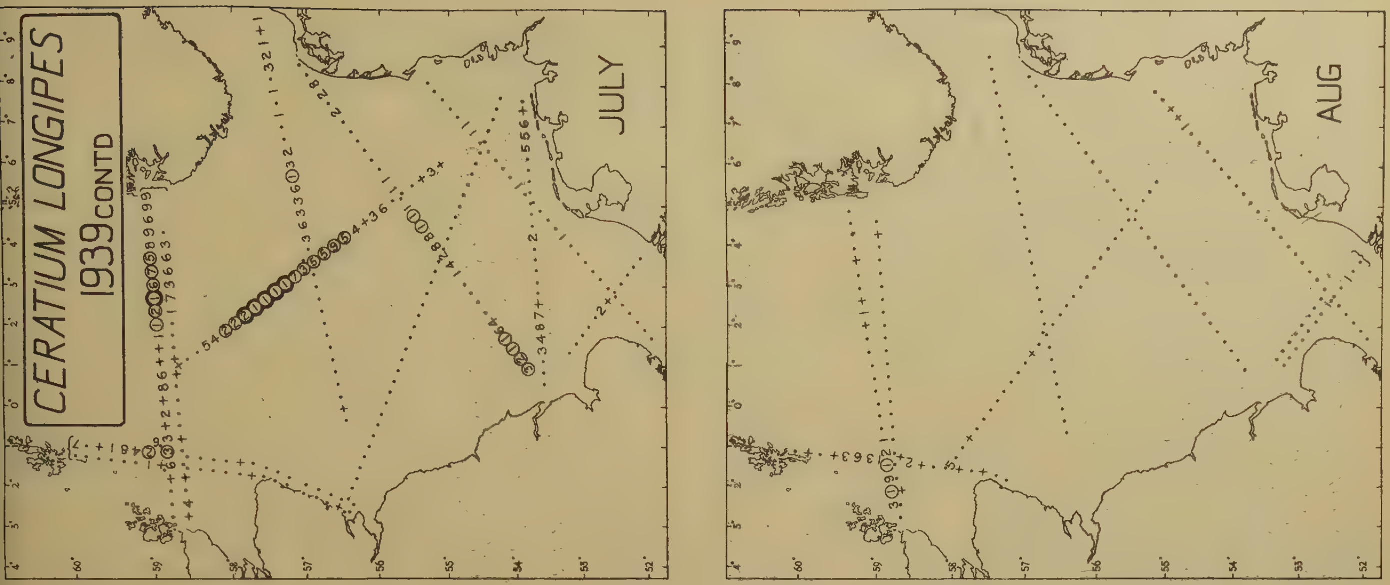
PLATE LVIII

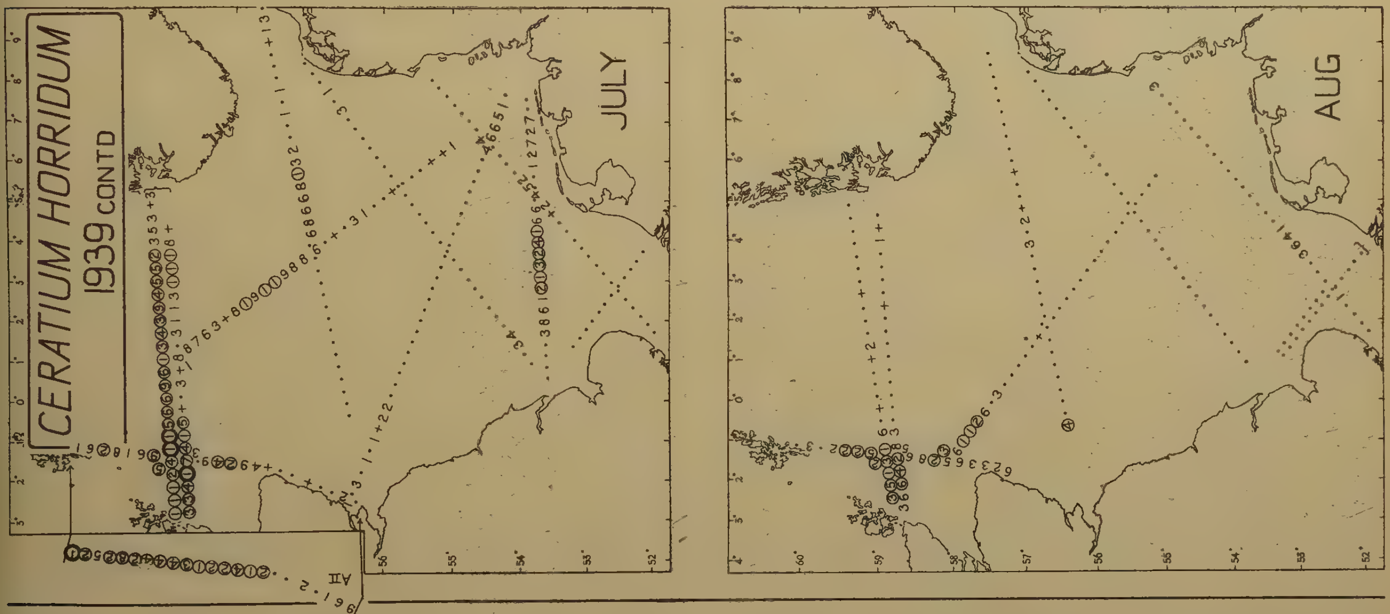


CERATIUM HORRIDUM
1939

JAN
FEB
MAR
APR
MAY
JUNE
A II

PLATE LIX


CERATIUM LONGIPES
1939 CONTD
JULY
AUG


CERATIUM HORRIDUM
1939 CONTD
JULY
AUG

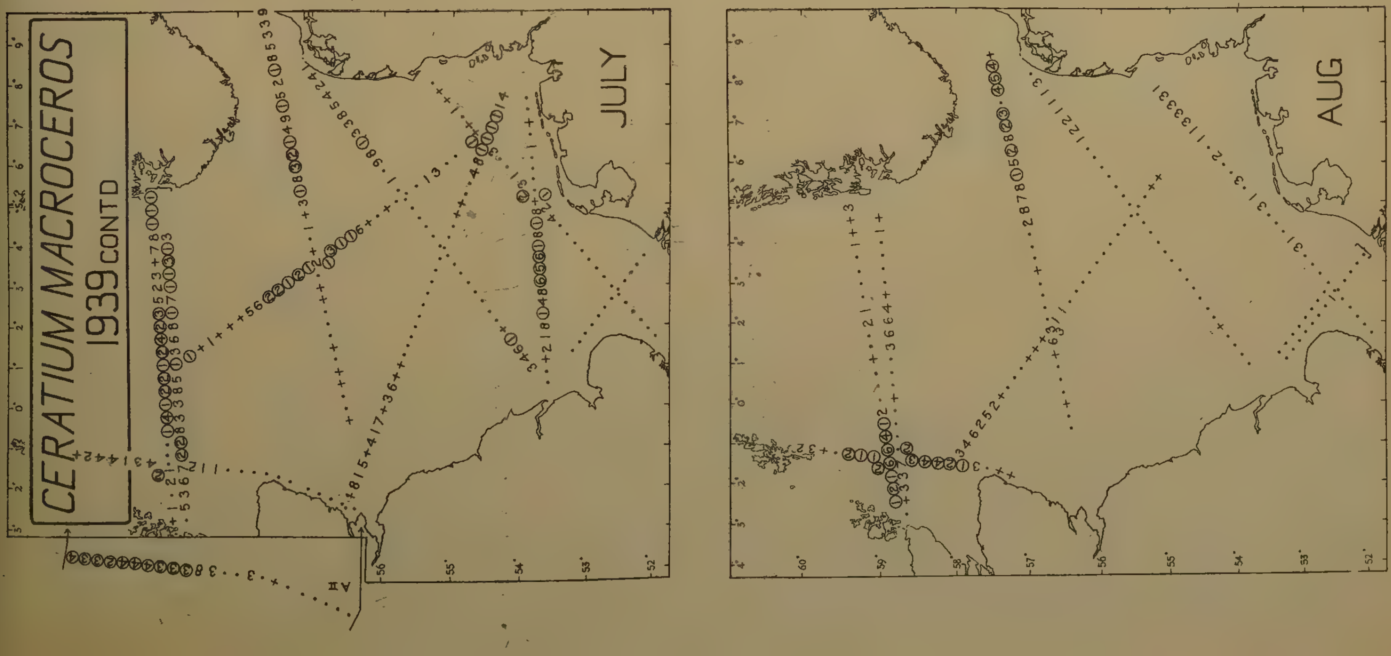
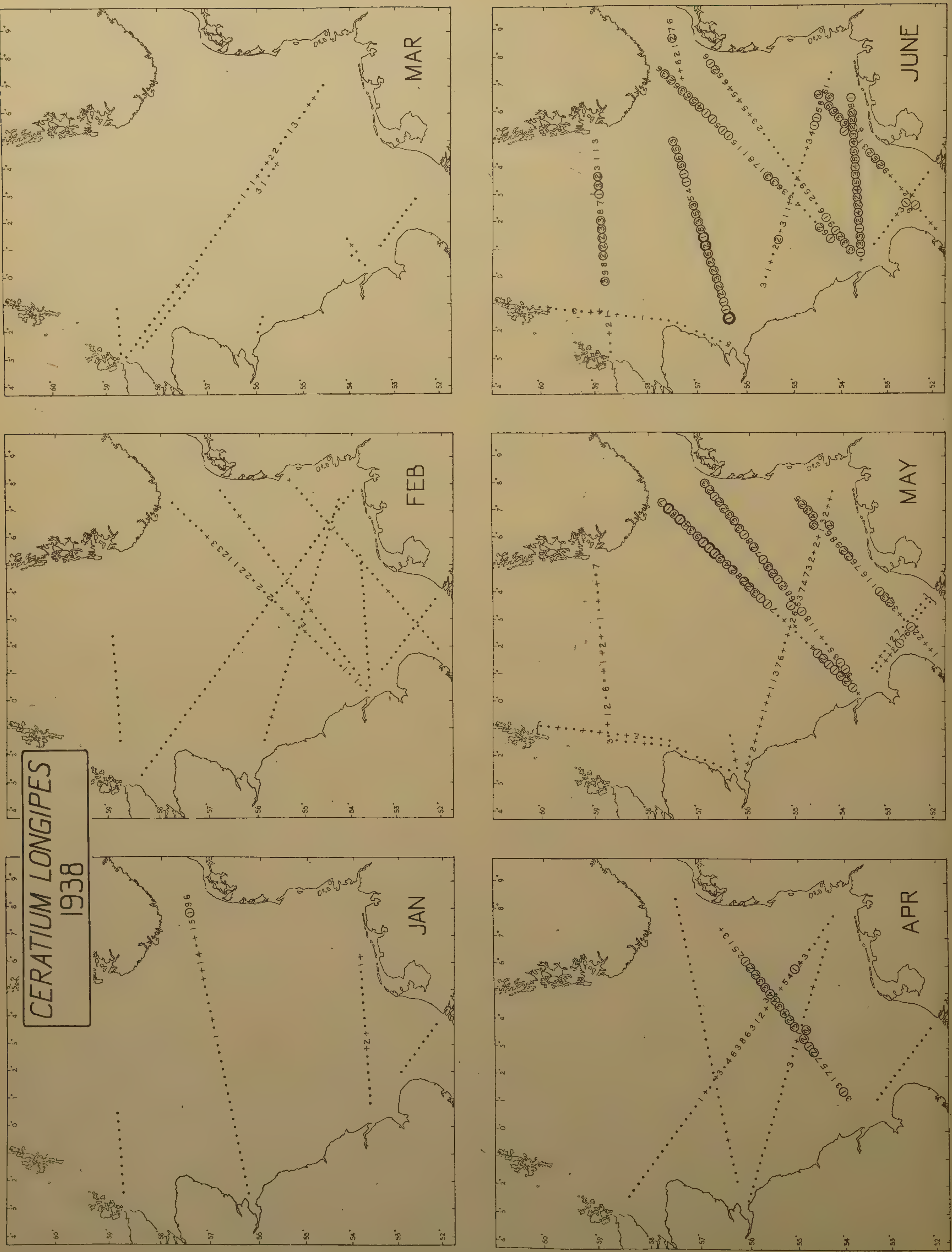

CERATIUM MACROCEROS
1939 CONTD
JULY
AUG

PLATE LX


MAR
JUNE
FEB
MAY
JAN
APR
60°
59°
58°
57°
56°
55°
54°
53°
52°

CERATIUM LONGIPES
1938

PLATE LXI

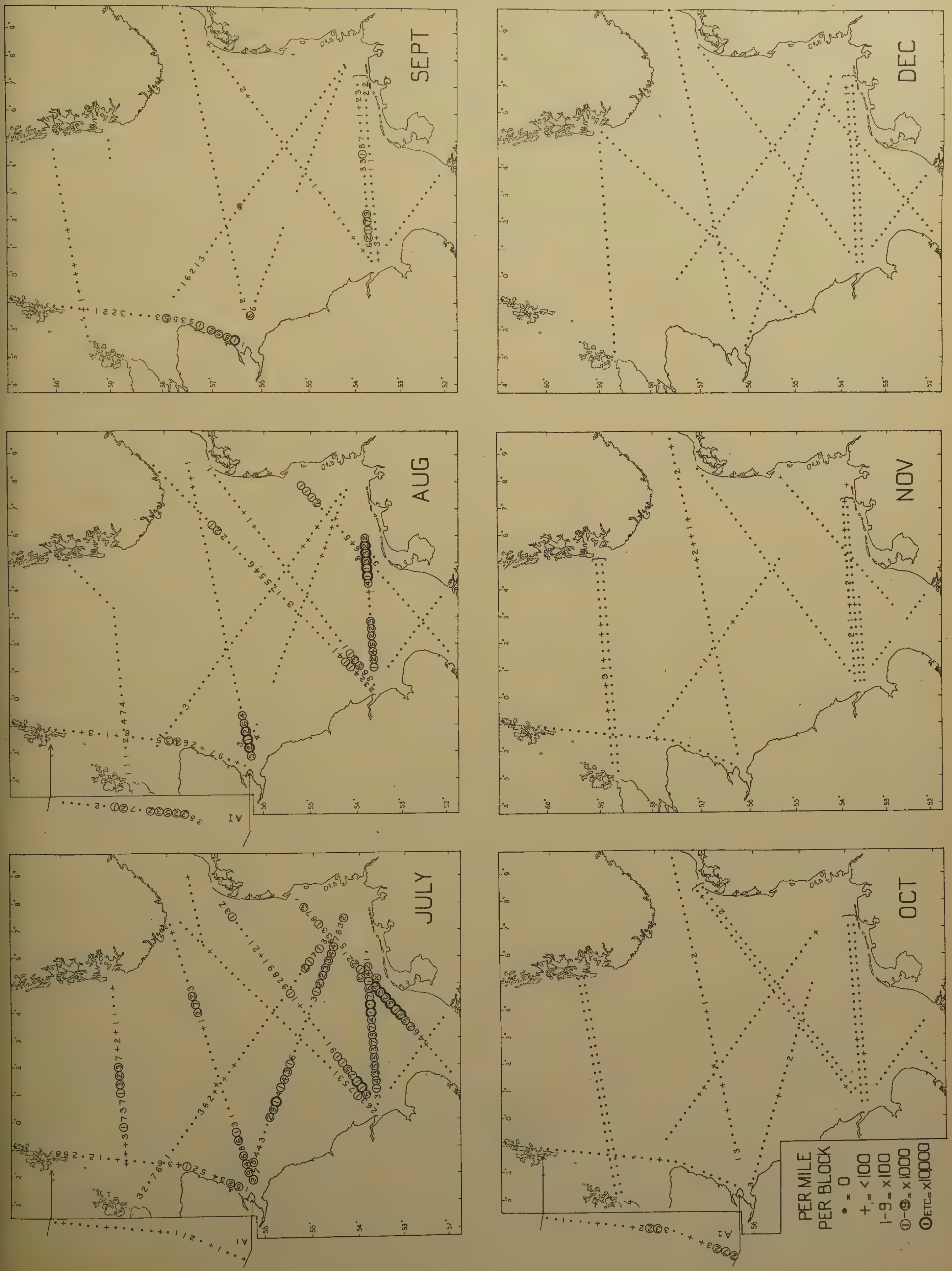
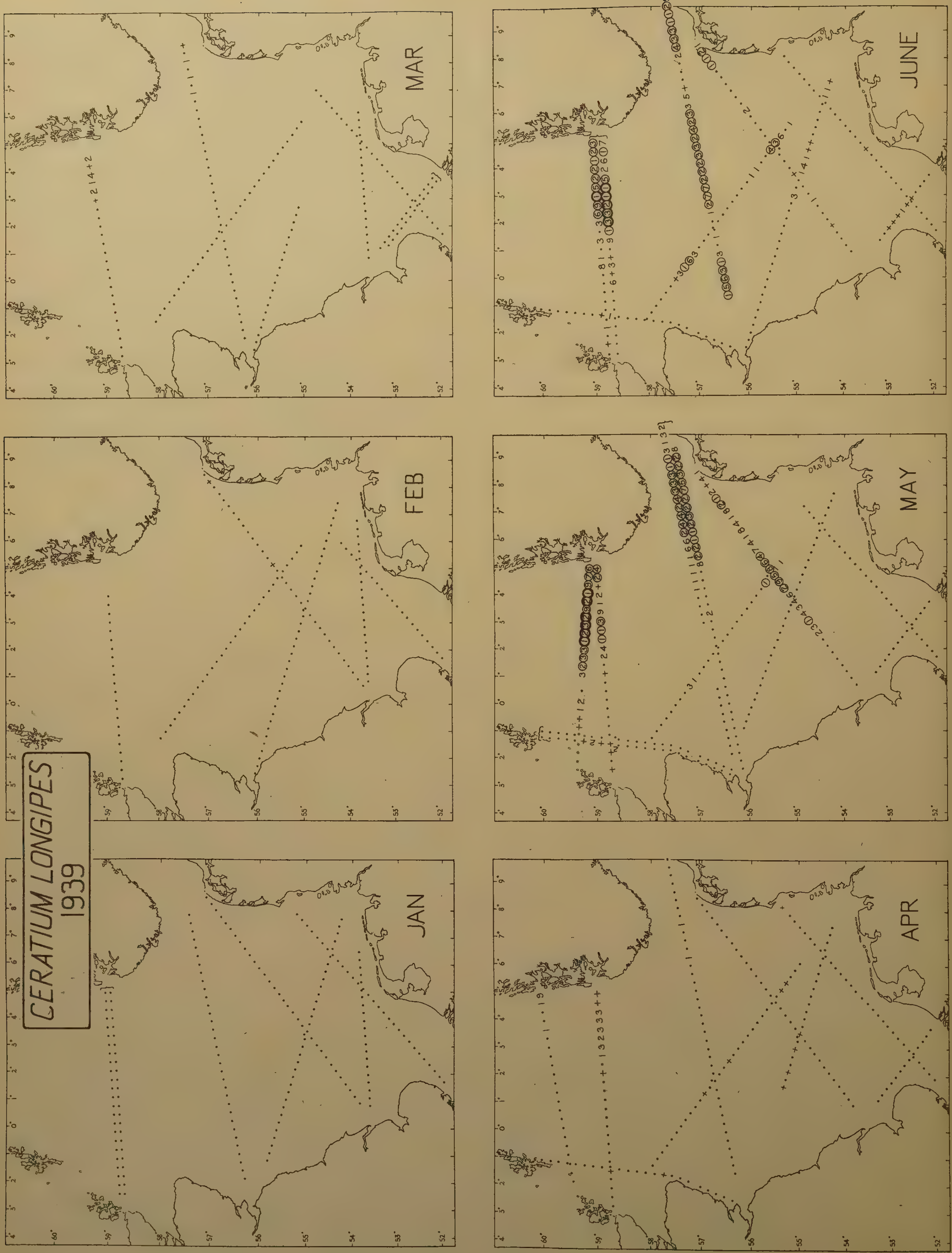

SEPT
AUG
JULY
DEC
NOV
OCT
AI
PER MILE
PER BLOCK
• = 0
+, . = <100
1-9 = x100
①-⑨ = x1000
①ETC = x10,000

PLATE LXII



CERATIUM LONGIPES 1939

JAN
FEB
MAR
APR
MAY
JUNE
60°
59°
58°
57°
56°
55°
54°
53°
52°
4°
3°
2°
1°
0°
1°
2°
3°
4°
5°
6°
7°
8°
9°

[*Hull Bulletins of Marine Ecology, No. 10, Vol. II, pp. 71–94, April, 1942.*]

CONTINUOUS PLANKTON RECORDS:
THE FAEROE-SHETLAND CHANNEL, 1939

BY

C. E. LUCAS, B.Sc., N. B. MARSHALL, B.A., AND C. B. REES, M.Sc.

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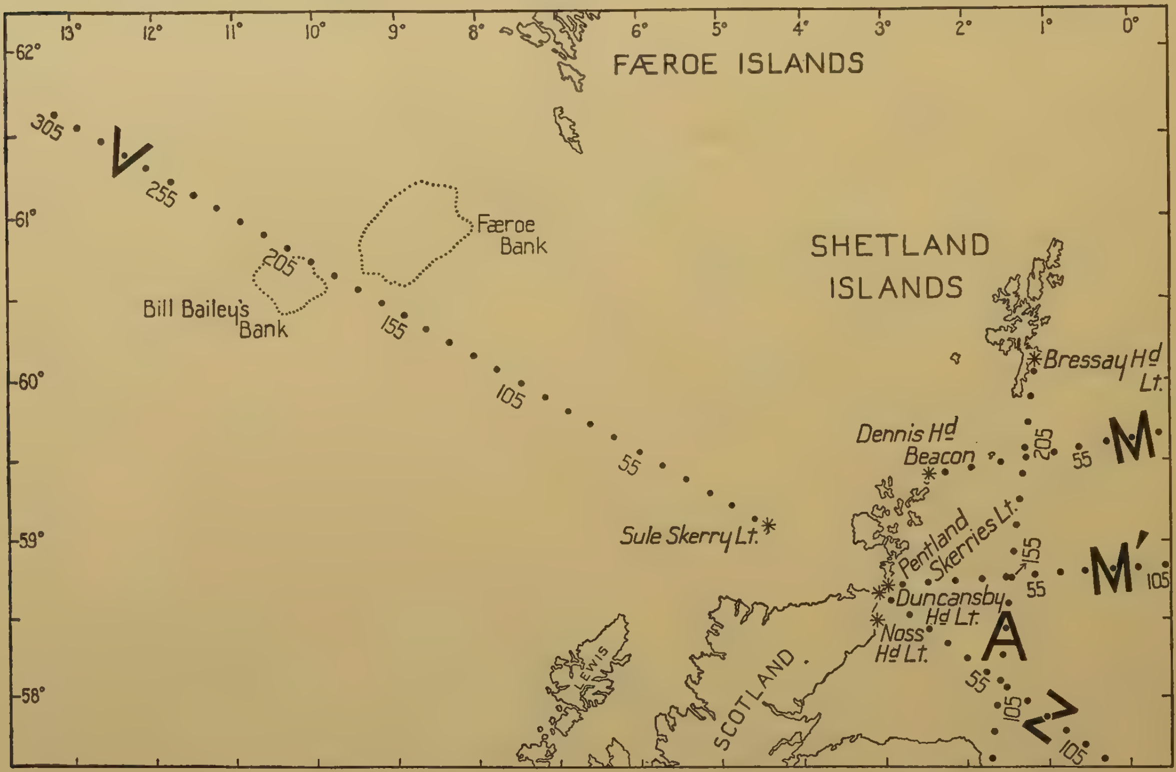
References 93

Introduction: Material and Methods.

Although the investigation of the North Sea plankton has been the immediate object of our surveys, we have always wished to extend the work into the Atlantic. Such records would add to the scanty knowledge of the plankton there and be even more useful in placing our North Sea data within a wider field of reference. When, in 1933, we obtained a number of records between Hull and the Pentland Firth, we also took an experimental traverse as the ship went on her way to Iceland (see Hardy, 1939, p. 4, and Anon., 1939, ‘Record List’). This remained an isolated record for some years, but soon after the survey of the northern North Sea was established we took the opportunity, through the kind assistance of the Icelandic Shipping Company, to start a new series of observations between the Pentland Firth and the Faeroe Bank.

The Icelandic Shipping Company's S.S. *Gulfoss* normally runs from Leith to Reykjavik (*via* the Pentland Firth and Vestmann Islands); as a trial, we arranged for a recorder to be towed for 300 miles from Sule Skerry towards Iceland (Text-fig. 1). The route thus crosses the southern entrance to the Faeroe-Shetland Channel and stops some 100 miles past the Faeroe Bank. The first record was made on 2nd April, 1939, and six had been obtained when the onset of war stopped the work at the end of August. This is a short series of records, and not sufficient to allow us to make the comparisons which we hoped for between the plankton of the north-western North Sea and the adjacent part of the Atlantic. On the other hand, they provide for the first time a series of continuous records at fairly short intervals from spring to midsummer, and it may be useful to present the data in some detail, so that they may provide a basis for future work.

Full details of the records will be seen in Table I. The last one (August) was not returned to us until well after the beginning of the war and the usual details of shooting, etc., were absent. We are able to state the day of shooting with some certainty (this is not likely to be more than one day in error), but the positions of shooting and hauling have had to be estimated from previous experience. Normally the instrument was shot off Sule Skerry Light and, since the amount of silk used was little short of that expected for a standard tow of some 300 miles, it is assumed that it was put over there and towed for some 290 miles; the probable error is much less than ± 10 miles, and is not likely to exceed ± 20 miles in any one place.


13°
12°
11°
10°
9°
8°
6°
5°
4°
3°
2°
1°
0°
62°
61°
60°
59°
58°
FÆROE ISLANDS
Færoe Bank
Bill Bailey's Bank
SHETLAND ISLANDS
Bressay Hd Lt.
Dennis Hd Beacon
Sule Skerry Lt.
Pentland Skerries Lt.
Duncansby Hd Lt.
Noss Hd Lt.
SCOTLAND
LEWIS
V
305
255
205
155
105
55
M
205
55
M'
155
55
105
A
55
105
Z
105

TEXT-FIG. 1.—Chart showing the course of the Faeroe-Shetland line (" V ") and its spatial relation to the neighbouring ends of the North Sea lines (A, M, M' and Z, see Hardy, 1941). The distances along the lines are shown in miles at 10-mile intervals, representing distances of 5, 15, 25 . . . miles from the Sule Skerry Light, and marking the mid-points of the standard " 10-mile blocks " used in analysis.

The usual methods of analysis were employed and are described (together with the limitations of the various methods) by Lucas (1941), Marshall (in the press) and Rae and Rees (in the press). The whole of the data has been worked up by the staff of the Leith Laboratory (phytoplankton by C. E. L., Copepoda by C. B. R., and zooplankton other than Copepoda by N. B. M.).

Since these data are rather isolated from those of the rest of the survey, the methods of presentation have varied a little. They are shown for the six records in tabular form in Text-figs. 2–5, symbols and numbers being used to denote the varying quantities on a principle similar to that for the North Sea data (*e. g.* Lucas, 1941): the numbers are given for each "block" of ten miles, starting from Sule Skerry (scale of miles above each column); below are depth diagrams for the route showing the different banks. In view of the possible influence of night and day on the apparent distribution of the plankton sampled at one level, we have shown the occurrence of sunset and sunrise for the different records (Text-fig. 4, where night appears as white dots on black and day as black dots on white). The records have been numbered I to VI in order of date.

Table I.—*Showing the Dates, Times and Positions of Shooting, etc., for the Six Records across the Faeroe-Shetland Channel in* 1939.

Number of Record.	Date.	Time (G.M.T.).		Position of start.	Mileage recorded.	Miles per section.	Wind.	Sea.	Weather.	Remarks.
		Shot.	Hauled.							
I	2.iv	0616	*ca.* 2100	*292*	*ca.* 130	*ca.* 5·5	S.E. 4–5–4	5–4	—	D
II	20/21.iv	0554	0857	50	243	5·33	W.N.W., 6	6	Fair	—
III	20/22.v	2320	0105	6	302	4·72	Var. 2	2	Fine	—
IV	8/9.vii	1135	1257	*288*	288	4·94	N.E., 5–6	5	—	—
V	22/23.vii	1206	1356	0	306	5·40	N.W., 2–N.E., 4.	4	—	—
VI	*ca.* 19, viii	?	?	*ca.* 0	*ca.* 295	*ca.* 5·0	?	?	—	*

Italicized numbers in column 5 denote a journey *from* Iceland, and *vice-versa*. D denotes a mechanical defect resulting in a stoppage of the mechanism. * no exact date; see text, p. 72.

In Text-figs. 2–5 the different species are shown without bias, but in order to see how they occurred together, selected ones are grouped in Text-fig. 6 to show the possible ecological relationships. Results from the six records are arranged in sequence, across facing pages, so that all can be seen together. The species are grouped more or less in order of appearance in time. Some have been graphed in the usual manner (*e. g. Rhizosolenia alata*), whilst only the major quantitative changes have been given for others by the use of lines of varying width (*e. g.* Thysanoessa spp.). Since the route appears to pass through waters of very different flora and fauna, this method will show at once how the species are grouped in relation to these, and how continuous recording can be used for the study of such communities.

The symbolic presentation of the various distributions has been left as far as possible to speak for itself. The sections on distribution serve to emphasize a few points of significance, to mention some few species which have not been illustrated and to relate some of the present data to those for the North Sea. Accounts of the

North Sea data are given by Lucas (1941 and 1942) for the diatoms and flagellates respectively, Rae and Rees (in the press) for the copepods, and Marshall (in the press) for the other zooplankton forms.

DISTRIBUTION OF THE DIATOMS.

The dominant diatoms were Thalassiosira spp. (including, probably, significant numbers of *Coscinosira polychorda*) and Chaetoceros spp. In addition *Rhizosolenia hebetata semispina* was relatively abundant in the third record, *Thalassiothrix longissima* in the fourth, *Thx. nitzschioides* in the fifth and *R. alata* in the sixth. In view of their small size we must also consider that Nitzschia spp. must have been very abundant in records IV to VI, whilst, owing to the mesh of the collecting silk used in this work (60 meshes to the inch), it is likely that other of the smaller species may have been more abundant than indicated here (*cf.* also Lucas, 1941, p. 22). Of all these, Thalassiosira spp. was the most striking owing to its persistent occurrence in high numbers.

Coscinodiscus spp. (not illustrated).

Only a few cells were definitely recorded, although it is possible that some of the isolated cells identified as Thalassiosira in the first record were really small Coscinodiscus. If this should be so they would provide evidence of the typical sparse " disco-plankton " found here by other workers in the winter and early spring.

Thalassiosira spp. (including *Coscinosira polychorda* (Gran.)). (Text-figs. 2 and 6.)

Whilst there may, as suggested above, have been some small Coscinodiscus spp. amongst the cells identified as Thalassiosira in the first record, yet Thalassiosira was one of the typical diatoms then, and its disappearance (except at the eastern end of the line) in the next record is an interesting feature. The eastern patch is similar to ones found at the other side of the Orkneys at that time, but whereas few appeared later near Sule Skerry, they were present in fair numbers in the neighbouring North Sea until August at least. The group was surprisingly sparse in early July and, whilst generally one of the dominant diatoms on this line during this period, it rarely attained the densities found in the North Sea.

Corethron criophilum Castr. (Text-fig. 3.)

The patch off Sule Skerry in July preceded a rather thinner one on the Leith-Lerwick line in August when, however, it was not recorded here. The present patch is decidedly the densest found during the whole recorder survey since its beginning in 1931.

Rhizosolenia alata Brightw. (Text-figs. 2 and 6.)

Reference to Plate XVII in 'Bulletin' No. 8 (Lucas, 1941) shows that *R. alata* was almost absent until June over the whole North Sea in 1939, although near the Pentland Firth it increased rapidly in July and August. It is noteworthy that whereas the f. *gracillima* was dominant in the North Sea, here the f. *typica* was by far the most abundant. The f. *indica* was not seen.

Rhizosolenia styliformis Brightw. (Text-figs. 2 and 6.)

These were usually of the smaller size found in the northern North Sea (Lucas, 1941, p. 29). Few traces were found near Sule Skerry, and these appeared later than those found on the North Sea side of the Orkneys. Although the numbers for the whole line were small, there appeared to be a definite maximum in July, as compared with April in the north-western North Sea.

Rhizosolenia hebetata semispina (Hensen). (Text-figs. 2 and 6.)

Whilst we found moderate numbers in the North Sea off the Orkneys, they were remarkably scarce at the eastern end of the present line. Where they were abundant, however, the maximum occurred in May as in the adjacent North Sea.

Chaetoceros spp. (Text-figs. 2, 3 and 6.)

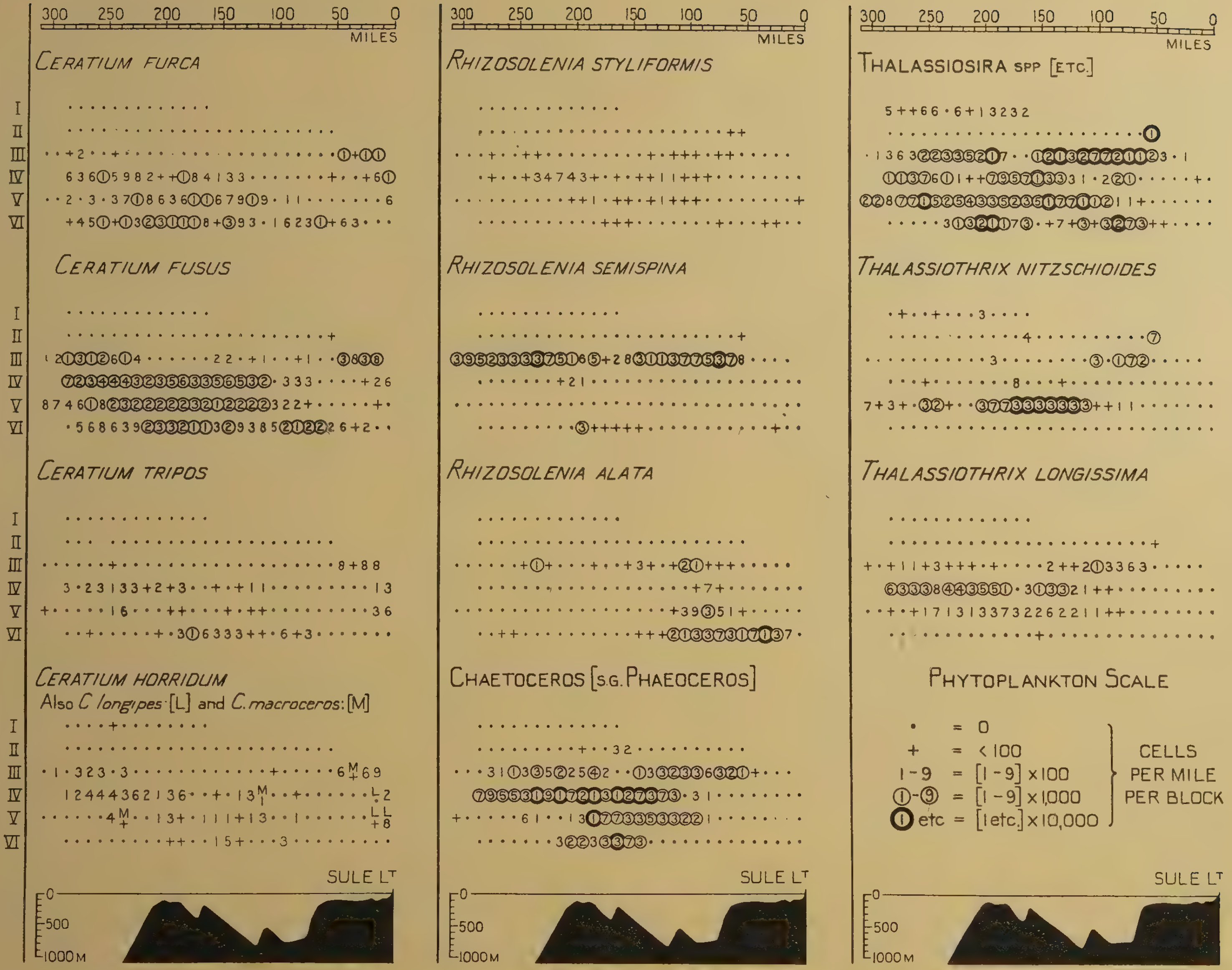
Although abundant along the rest of the line, these were very scarce near Sule in contrast to the large numbers found on the other side of the Orkneys from April to July. *Chaetoceros decipiens* Cleve has been separated from the remaining Hyalochaetes, and it is interesting to note the mutual exclusion of the two categories, both in time and space. When compared with the North Sea results it is seen that only the Phaeocerids (mainly *Ch. borealis* Bailey) were more abundant on this line.

Thalassiothrix longissima Cleve and Grun. (Text-figs. 2 and 6.)

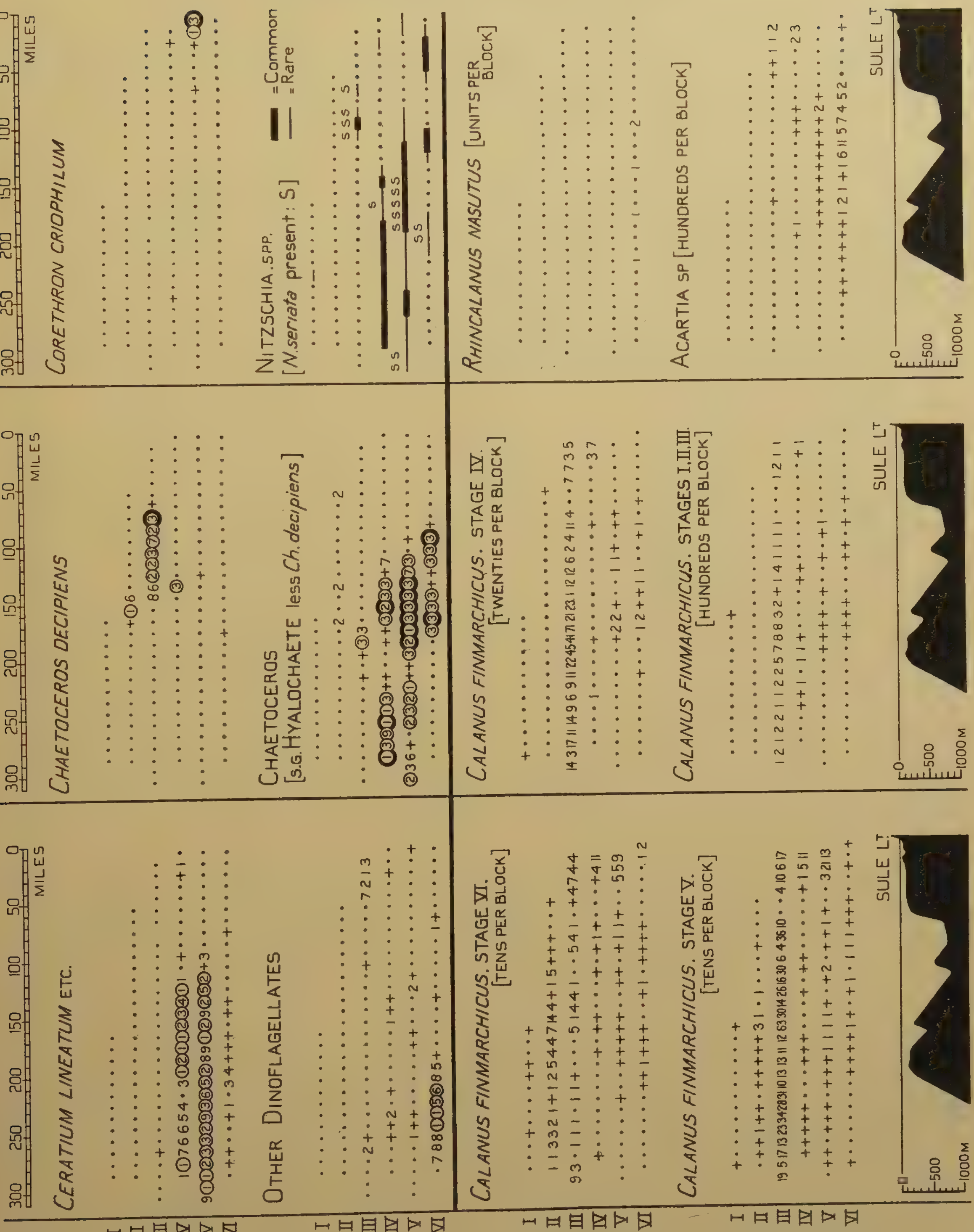
The patches found in July were much denser than any of the North Sea samples of 1939, with the exception of the patch near Bergen in March.

Thalassiothrix nitzschioides Grun., Van Heurck. (Text-figs. 2 and 6.)

The moderate patch found near Sule Skerry in May corresponds to the patches found on the other side of the Orkneys from March to May, although less dense; but from May to July the eastern limit was found further from Sule until, after the maximum at the end of July, it suddenly became absent along the whole line. It similarly decreased at the approach of summer in the North Sea, both in 1938 and 1939.



TEXT-FIG. 2.—Showing the changing numbers of eleven phytoplankton organisms on each 10-mile block for six records along the Faeroe-Shetland line between April and August, 1939 (I–VI, see Table I). A general scale for phytoplankton is shown in the bottom right-hand corner. The blacked-in graphs below show the varying depth along the route.



TEXT-FIG. 3.—Showing the changing numbers of six phytoplankton organisms and three copepods along the Faeroe-Shetland line between April and August, 1939. See also legend to Text-fig. 2

Gyrosigmoids. (Text-fig. 6.)

This group includes all the sigmoid diatoms. They were very scarce except for an unusually dense western patch (relative to our other records) in early July.

Nitzschia spp. (Text-fig. 3.)

In view of the previous findings in this area it is possible that many of the small Nitzschia spp. which have been so common were *N. delicatissima* Cleve, but this is by no means certain ; they cannot easily be distinguished from the slender forms of *N. closterium* (Ehr.), which were also present. Forms such as these were abundant in July and August, and *N. seriata* Cleve, whilst by no means as common, was yet fairly abundant in May and July. It seems noteworthy that these very small diatoms can be caught in appreciable numbers in spite of the absence of any significant quantity of Phaeocystis (*cf.* Lucas, 1940, p. 128).

In addition to those mentioned above, *Paralia sulcata* Ehr. was found only on the first record, along with traces of *Ditylium Brightwelli* (West), *Biddulphia aurita* (Lyngb.), *Leptocylindrus danicus* Cleve and *Streptotheca thamensis* Shrubs. Although the actual numbers were quite small, *Skeletonema costatum* (Greville) was relatively quite abundant on this record. *Rhizosolenia Shrubsolei* Cleve, *R. stolterfothii* H. Pérag. and *Biddulphia sinensis* Grev. all appeared in late April ; Dactyliosolen spp. in May and early July ; Navicula spp. at the end of July ; *Lauderia borealis* Gran in July and August, as well as further traces of *R. Stolterfothii.* Of these, *B. sinensis*, Skeletonema, Leptocylindrus and Lauderia were recorded as more abundant in the north-western North Sea, and it seems important to note that *Asterionella japonica* Cleve and Moller, *Rhizosolenia faeröense* Ostenf. and *Cerataulina Bergonii* H. Pérag., which were all quite abundant near the east coast of the Orkneys, were not found on the present line.

DISTRIBUTION OF THE DINOFLAGELLATES.

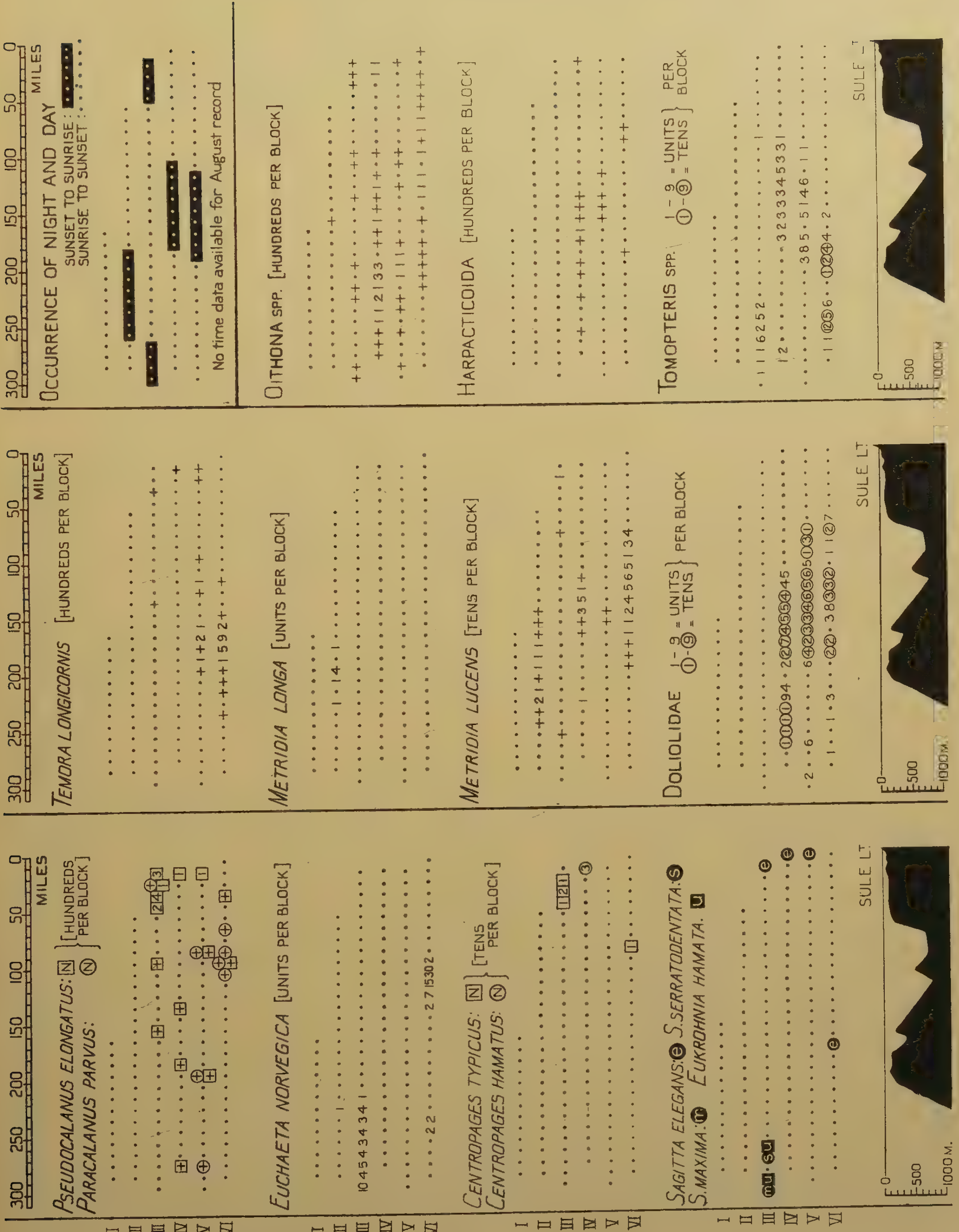
It is striking that in contrast to the north-western North Sea only two species of major importance were found here. These were *Ceratium fusus* and *C. lineatum* (etc.).

Ceratium fusus (Ehrenberg). (Text-figs. 2 and 6.)

Although one of the major forms here, *C. fusus* only reached about one-tenth of the densities recorded in the neighbouring waters of the North Sea. Off Sule Skerry they were only abundant in May, in contrast to the North Sea maximum in July and August ; elsewhere the maximum was in early July.

Ceratium lineatum (etc.). (Text-figs. 3 and 6.)

In view of the well-known difficulties of separating this species from similar



TEXT-FIG. 4.—Showing the changing numbers of ten copepods and six other zooplankton groups along the Faeroe-Shetland line between April and August, 1939. The incidence of night and day is shown graphically for comparison in the top right-hand corner. See also legend to Text-fig. 2.

species and the aberrant forms of *C. tripos*, etc., it was decided to combine all these under the one head. They attained densities similar to those of *C. fusus*, but had a maximum at the end of July, decreasing abruptly in August. They were scarce at the eastern end, although elsewhere they were on the whole commoner than in the North Sea.

Ceratium furca (Ehrenberg), *C. tripos* O. F. Müller and *C. horridum* Gran were very scarce, both in comparison with the previous species and with their own numbers in the North Sea (Text-fig. 2). *Ceratium macroceros* (Ehrenberg) and *C. longipes* (Bailey) only appeared as rare traces in these records. The local rarity of the former has been mentioned earlier (Ostenfeld, 1931), but *C. longipes* seems to have been unusually scarce, although neither were as common in the north western North Sea as the other species. The remaining Dinoflagellates (mainly Peridinium spp. and Dinophysis spp.) were also scarce in comparison with those found on the other side of the Orkneys, and did not attain appreciable numbers until a western patch appeared in August (Text-fig. 3).

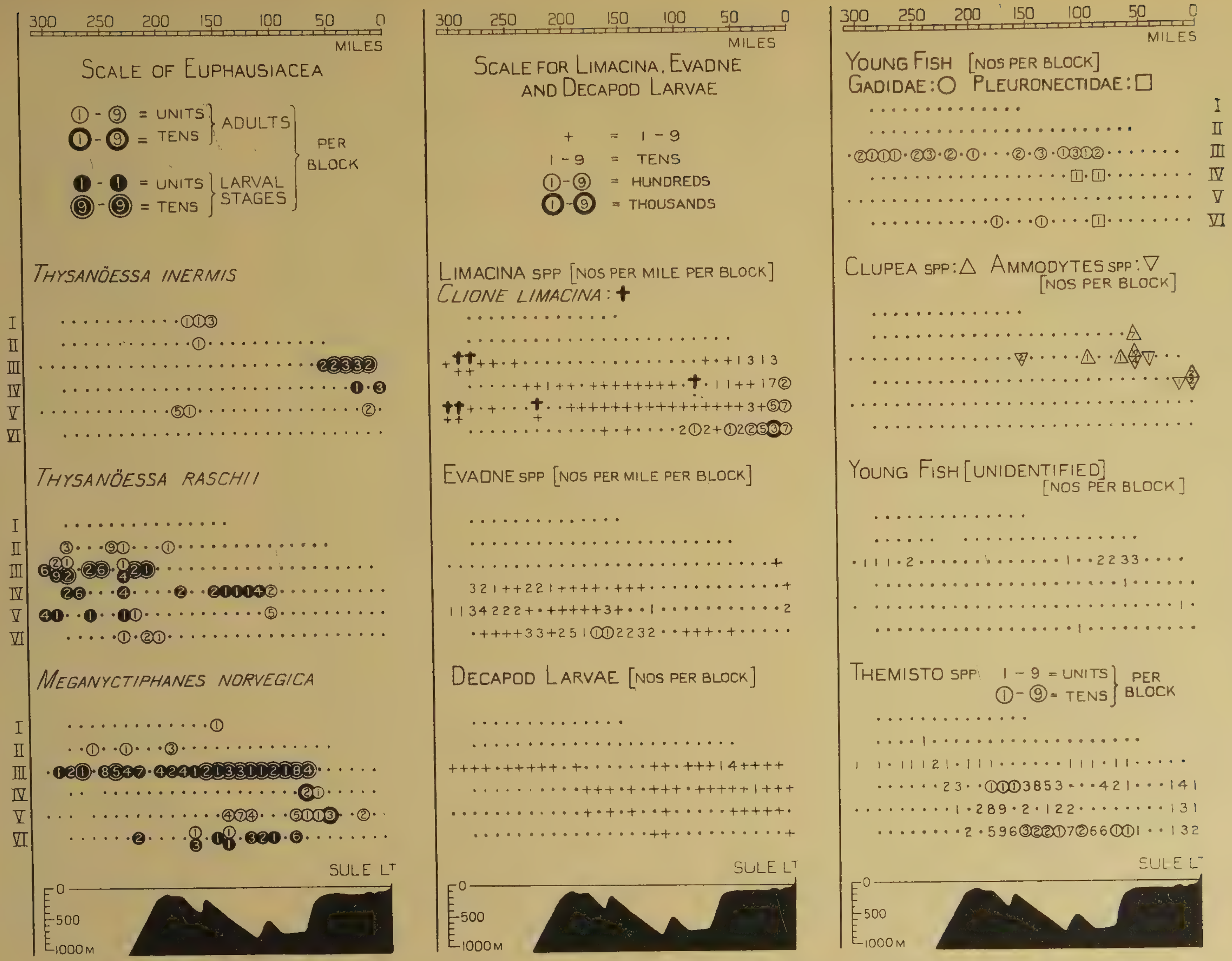
As a whole the group was distributed in two distinct areas; those off the Orkneys became progressively scarcer after May, and more limited in area, whilst the others increased up to July at least and seem to have extended further east as the season progressed. Thus, the coastal band, which might have been expected to have had the closest affinity with the North Sea patches, had its maximum in May instead of July or August as in that region.

Whilst considering these flagellates, it is worth mentioning that, although there may have been very small quantities of Phaeocystis, no significant patches were seen (for "significance" see Lucas, 1940, p. 149); nor were any colonies of Halosphaera seen.

DISTRIBUTION OF THE COPEPODA.

The copepod distribution is shown in Text-figs. 3, 4 and 6. *Calanus finmarchicus* was definitely the most abundant, with Acartia spp. second, followed by *Temora longicornis* and Oithona spp. The others were much scarcer, except for a small patch of *Pseudocalanus elongatus* in May.

In conformity with the North Sea survey, the species *Calanus finmarchicus* Gunn. was subdivided into the following groups: Stages I, II and III combined, St. IV, St. V and St. VI (adults). Owing to the short period of the survey little useful information is available concerning the life-history of Calanus in these waters. However, it is clear that the largest numbers of St. VI were found at the end of April, whereas the maximum of all the younger stages was found in May. On the other hand, as with much of the plankton, it is possible to separate a coastal zone from the rest of the line (see p. 84) and there are differences between these. Over the rest of the line there is only one definite maximum, but at least for St. V and VI there appear to be two near Sule, although it is by no means certain whether these are the results of the life-cycle or of possible water movements. As



TEXT-FIG. 5.—Showing the changing numbers of some other zooplankton groups along the Faeroe-Shetland line between April and August, 1939. See also legend to Text-fig. 2. The incidence of night and day is shown in Text-fig. 4.

a whole Calanus was scarcer on this line, particularly in the east, than in the adjacent parts of the North Sea.

The remaining copepods can be divided into two groups: those which were mainly coastal and those which were over deeper water. *Centropages typicus* Kröyer and *C. hamatus* Lilljeborg were mainly coastal and had maxima in May and early July respectively; *Pseudocalanus elongatus* Boeck was similar, with a maximum in May. Whilst Acartia spp., Oithona spp. and Temora were present there, the greater numbers were over the deeper waters with maxima in August and early July respectively. *Paracalanus parvus* Claus, *Metridia lucens* Boeck and the Harpacticoida were almost entirely limited to the region of the deeper waters, whilst *Rhincalanus nasutus* Giesbrecht, *Euchaeta norvegica* Boeck and *Metridia longa* Lubbock were quite absent in the coastal band. Amongst these we may note that Rhincalanus only appeared in August and *M. longa* mainly in late April, whilst Euchaeta had two quite distinct maxima in May and August. With the exception of *M. longa*, Euchaeta and Rhincalanus, these species were all more abundant in the neighbouring North Sea. In addition to these mentioned *Candacia armata* Boeck was once found (near the coast in May). It is perhaps worth mention that *Calanus hyperboreus* Kröyer was not even recorded once.

DISTRIBUTION OF THE OTHER ZOOPLANKTON.

Next in importance to Calanus, the most obvious members of the zooplankton were Tomopteris spp., Limacina spp., Evadne spp., Themisto spp., various Euphausiacians and the Doliolids.

Chaetognatha. (Text-fig. 4.)

Very few of these were found, but their distribution is of interest. With one exception *Sagitta elegans elegans* Verrill was confined to the most easterly blocks; the exception occurred over the Faeroe Bank. *S. setosa* J. Müller was not recorded. The remaining three species were restricted to the western end of the line (in May) and comprised isolated individuals of *S. maxima* (Conant), *S. serratodentata* Krohn and *Eukrohnia hamata* (Möbius). This distribution agrees very well with that of Fraser (1937 and 1939), except that, possibly as the result of taking vertical hauls, he found *S. serratodentata* in waters nearer the coastal zone.

Limacina spp. (Text-figs. 5 and 6.)

Although complete identification has not been possible, by far the greater part of these have been *L. retroversa* Flemming, and probably the whole of them. The marked restriction of the patches to the coast is striking, and it is noteworthy that this is the only form to be largely restricted to the coastal area, which increased as the season progressed. The bulk of the coastal patches consisted of small and growing stages (although some large ones were present), whereas most of the scattered animals over the deeper waters were larger.

Euphausiacea. (Text-figs. 5 and 6.)

In order to estimate the possible significance of vertical migration in this work, the occurrence of night and day is shown in Text-fig. 4 for comparison with the data for these and other animals. It is likely that there may be some influence upon the vertical distribution of the Euphausiacians, as the results from the North Sea show (Marshall, in the press): the present evidence suggests, however, that there was little connection between the incidence of night and day and the distribution of the young or the adults. Such results permit us to have more confidence in the apparent distributions, and it will be seen that the very differences between the species points against the effects of diurnal migration.

Thysanoëssa inermis Kröyer was most abundant near the coast and over the Faeroe Bank, *Th. raschii* (M. Sars) mainly in the waters to the west of the Bank, and *Meganyctiphanes norvegica* (M. Sars), although widespread except near the coast, on the whole was commonest where the others were scarcer. This suggests a tendency for them to be mutually exclusive.

The distributions of the adults and the larvae at 10 metres are shown together in Text-fig. 5. In all three species a preliminary period with adults only in April is followed by an outburst of larvae in May. The larvae of the Thysanoessa spp. persisted in smaller numbers into July (although not necessarily in the same place), to be followed later by a few adults. Of Meganyctiphanes there were only adults in July, giving place mainly to small numbers of larvae in August. In such a short survey it is not possible to say with any certainty whether these were separate breeding periods or whether the sequence was due to water movements, but the former seems likely. It is significant that Macdonald (1928) found two spawning periods for *Th. raschii* at similar times to those apparently shown by Meganyctiphanes here, and it is likely that more larvae of this species might have been found had we obtained later samples. We should note that he also records (1927) that *Th. raschii* and *Th. inermis* were rarely found together in similar numbers in the Scottish lochs, either the one or the other being definitely dominant; in addition it was unusual, as we found for all three species, for the larvae and the adults to appear together in large numbers. All these points seem to be more characteristic of this line than in the North Sea, where the effects of diurnal migration seem to be more important.

Doliolidae. (Text-figs. 4 and 6.)

These were small forms and, owing to their crushed condition, it was not possible to identify them.[1] Note that the eastern patch seems to have retained its identity on the whole up to the end of August; its western edge in particular varied little during this time. None were found in the North Sea in our records in 1939.

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[1] We are indebted to Dr. J. H. Fraser (of the Fisheries Division, Scottish Home Department) for unpublished information that *Doliolum* (*Dolioletta*) *gegenbauri* Ulyanin and its var. *tritonis* are the only forms which have been recorded in this area so far. Thus it is likely that the present forms are similar to the species found in 1933 in the North Sea by Lucas (1933).

Young Fish. (Text-figs. 5 and 6.)

As a whole they had their maximum in May, when there were a number of clupeid larvae off the coast (largely herring), with gadoids over the deeper waters. Pleuronectids were generally scarce. It is probably that the damaged and unidentified specimens belonged mainly to these groups, although there may have been some of other species.

OTHER ZOOPLANKTON.

Tomopteris, Evadne and Themisto were most abundant in the last record, whilst the various decapod larvae were diffuse, but most abundant in May on the whole. Tomopteris, like Clione, was never found in the coastal waters, although few specimens of the latter were found, and only one of these (in the west) was anything more than juvenile. Radiolaria and Foraminifera, also Lamellibranch, Cyphonautes and Echinoderm larvae and Podon spp. were scarce on the whole and their distribution calls for no comment.

DISCUSSION: THE PLANKTON AS A WHOLE.

As one reviews the various species, it is not possible to miss the impression that their distributions were closely related to the conformation of the bottom. Broadly the route can be separated into four distinct areas—(1) a coastal zone of about 60 miles from Sule, (2) the deeper water of the channel between this and the Faeroe Bank, (3) a rather ill-defined region over the Bank itself, and (4) the much deeper water to the west of it. Many forms were limited or almost limited to one or other of these, whilst others were abundant in more than one, either at the same or different times. Those which were found mainly in one of these sections are as follows:

Shallow coastal zone: Corethron, *S. elegans*, Limacina, Pseudocalanus, *Centropages typicus* and *C. hamatus*, young *Th. inermis* and clupeid larvae.

Channel zone: *Chaetoceros decipiens*, Acartia spp., *Metridia lucens* and young Meganyctiphanes.

Bank zone: Calanus (St. I–IV), Temora and *Metridia longa*.

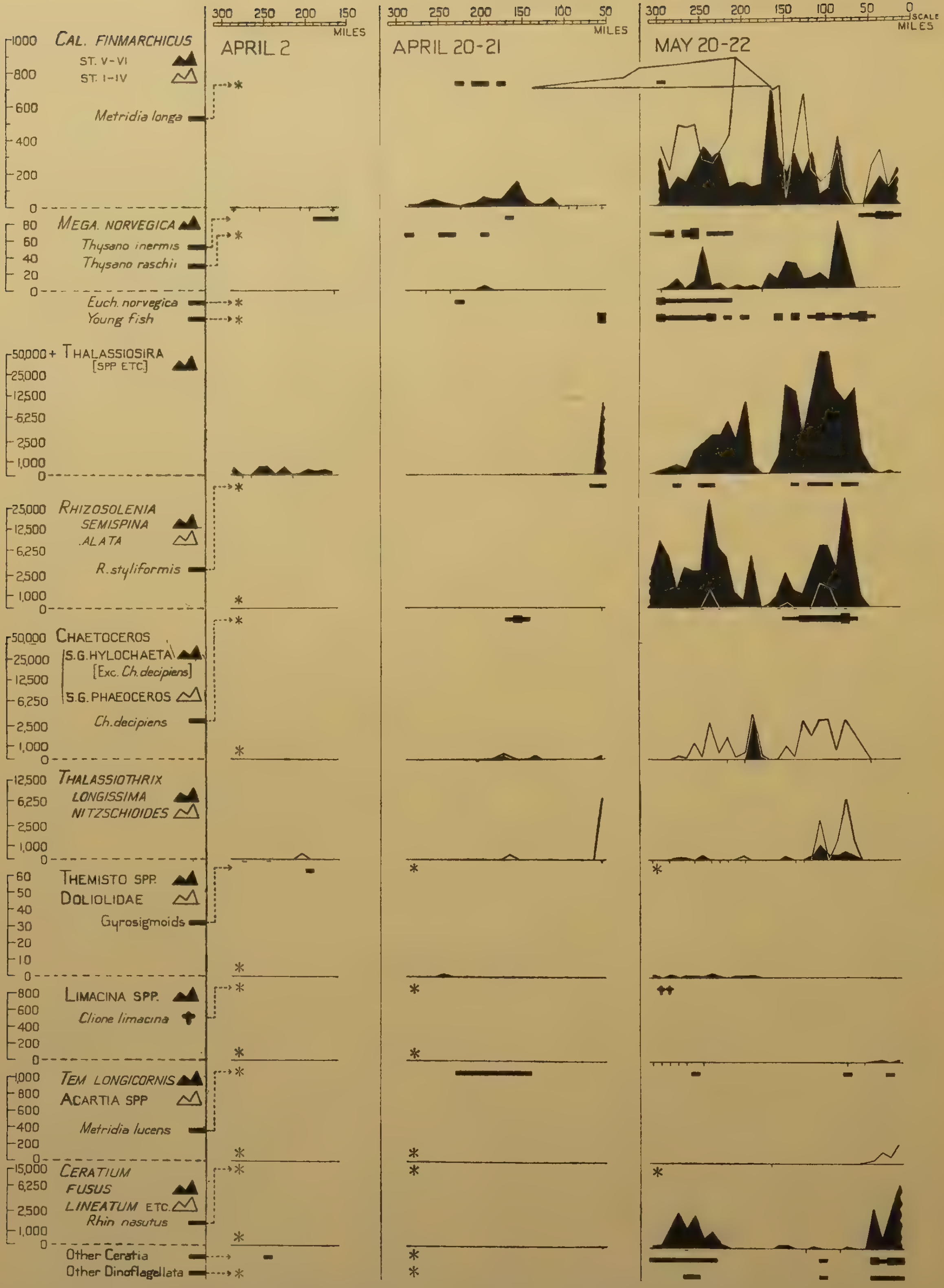
Deep water zone: *Rhizosolenia styliformis*, *Thalassiothrix longissima*, Dinoflagellates (other than Ceratia), *Sagitta serratodentata*, *S. maxima*, *Eukrohnia hamata*, Tomopteris, *Thysanöessa raschii* and, perhaps, Clione.

A number of other forms are more difficult to place, since they are not so restricted, but we may note that *Rhizosolenia semispina*, Euchaeta and the Doliolids were characteristic of the channel and the deeper water. Similarly the following, whilst they do not fit into any category, were usually scarce or absent in the coastal waters: the Hyalochaetes, Evadne, Rhincalanus and the Gadoid larvae. The whole suggests strongly the separation of the coastal zone from the rest of the line and the possible subdivision of the latter.

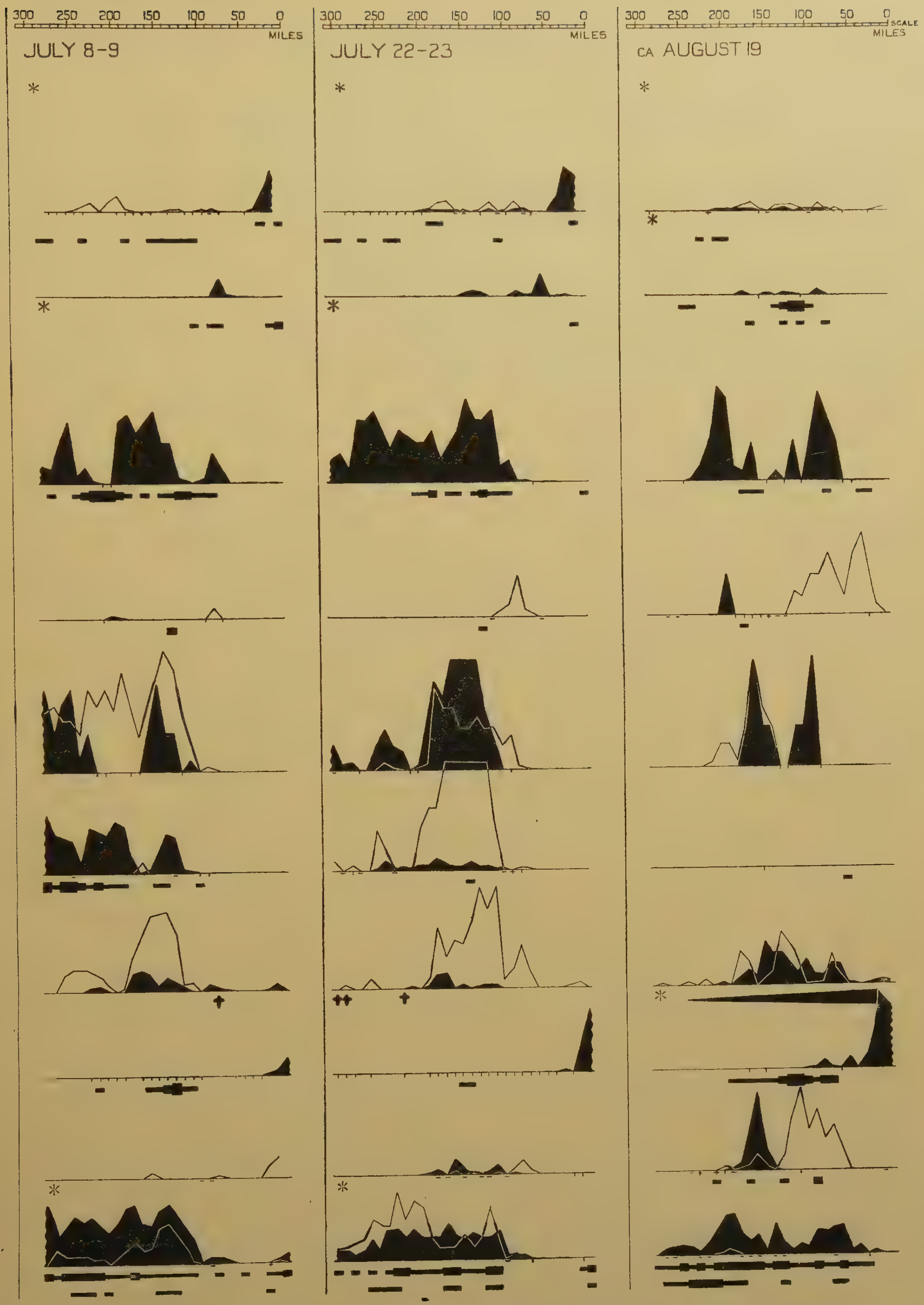
If now we turn to Text-figs. 6 and 7 we can see the changes in time. With few exceptions the most abundant forms are shown here, together with a few of the less abundant ones of particular interest. The general sequence, it may be noted, is quite different in the coastal waters from that elsewhere; only when the patch of *Rhizosolenia alata* in August extended over both the channel and the coastal waters was there any sign of close relationship, and even then this patch might be considered to be made up of two patches separated by a region of smaller numbers. It would be interesting to compare the results with those of other workers in the area using different methods but, except for the phytoplankton, this is rarely possible, and there is little detailed work from this area throughout the season. Even for the phytoplankton it is not easy to find suitable results for comparison, since much of the work has been done in waters a little to the north and much of it has been based on surveys separated by long time intervals.

Ostenfeld (1903) suggested that the phytoplankton off the Faeroes was similar to that in the neighbouring ocean with the addition of a variable number of neritic forms. A typical succession of " Disco- and Sphaeraplankton, Chaetoplankton, Styli- and Scotica or Longipes-plankton with a return to the winter Discoplankton" appeared to be constant, although the intervening neritic communities varied from year to year and place to place, being more marked nearer the islands. Paulsen's observations (1904, 1909 and 1918) on the whole confirmed and amplified these; in particular (1909) he observed that off the Faeroe Bank the phytoplankton would persist well into the summer. The only relevant part of Gran's famous survey of the phytoplankton in 1912 (Gran, 1915), although limited to June and situated well to the north of this survey, is yet of importance for his references to " oceanic " and " coastal " conditions. In particular his results showed how much greater and earlier may be the growths off the mainland and the islands than in the water between and beyond. Again, over the whole north-west " the plankton was here at most places an almost monotonous diatom-plankton " (p. 129) dominated by *Nitzschia delicatissima*. In the North Sea proper, however, it was then a Longipes plankton (May–June), the diatoms having largely disappeared.

Whilst Nielsen's survey (1935) is much more precise than any of the preceding ones, it is perhaps the most unsuited of all for comparison with the present work in view of his concentration on the nannoplankton. Undoubted though the imporance of this may be, the recorder survey has never set out to investigate it (as have few other surveys). In addition his various cruises were taken in different years. However, his general conclusions are relevant. He suggests that the phytoplankton production began in the Faeroe fiords in April, whilst in May the numbers over the Faeroe Bank were rather higher than elsewhere in the vicinity of this line. He also found that, at least up to July, the Bank and the channel waters usually were more densely populated. In contrast to this we can consider Hentschel's findings in 1935 (Hentschel, 1936), using methods which resemble more the usual ones.



TEXT-FIG. 6 —Showing the changing numbers of selected plankton organisms recorded by record along the Faeroe-Shetland line from April to August, 1939. The continuous vertical lines denote for each record the position 320 miles from the Sule Skerry Light, the scales above indicating the series of " 10-mile blocks " used in analysis. Some forms (*e.g. Calanus finmarchicus*) are shown

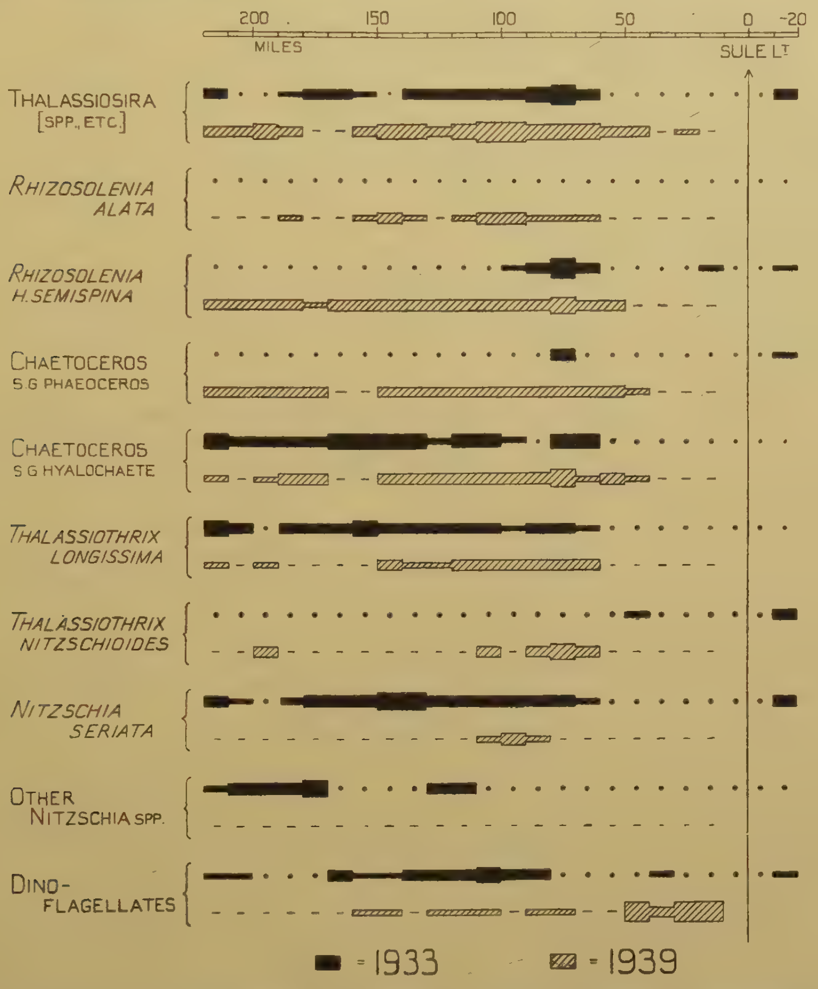


as blacked-in or open graphs, whilst others (*e.g.* Thysanoessa spp.) show the major patches by lines of varying width. The small vertical and horizontal strokes denote "traces" of the blacked-in and open graphs respectively. The symbol * denotes the absence of a particular form from that record. The organisms are arranged broadly in their order of appearance along the line.

In February he found very little phytoplankton, although this was slightly denser off the Faeroes than elsewhere, but in March he considered that the spring production had definitely begun, both off the islands and off the mainland of Shetland. Quite dense phytoplankton was found here, although in the waters between there had been little increase since February and the numbers were similarly low to the west of Faeroe. Once again we have to note that his samples were further to the north than ours, and so they should not be compared too closely.

In many points the present survey agrees well with the preceding ones and helps to confirm them, particularly since this work consists of a series of records taken *within five months*, whereas previous knowledge has had to be built up from series of isolated cruises. With the exception of the diffuse plankton found by us at the beginning of April (probably corresponding to the "disco-plankton" of Ostenfeld), we also found the first signs of the spring flora appearing over the Faeroe Bank and near the mainland (Orkney, in our work). After this initiation the diatoms increased and spread rapidly, only to decrease in July and August, giving place to a sparser, but quite appreciable dinoflagellate population. On the other hand, we found that after the initiation period and until the phytoplankton began to decrease in July and August, the diatoms were as dense or actually denser in the channel area than over the Bank and near the mainland coast. In fact the coastal area had very little phytoplankton after May, although it is interesting that some of the later diatoms to appear were found over the Bank before they occurred in the other waters, *e. g.* the Hyalochaetes (other than *Ch. decipiens*). *Rhizosolenia alata* was most abundant in the channel area until the last record, when it appeared to extend over the coastal waters, or to be connected with another patch there. It appears, then, that the channel may be quite as, or even more, productive than the Bank, thus agreeing rather more with the implications of Nielsen's findings than with those of earlier workers. On the other hand, our results, as well as the earlier ones, agree in showing that west of the Bank the numbers of diatoms were much lower, with the rare exceptions of *Rhizosolenia semispina* and *Thalassiothrix longissima*.

There are some other discrepancies, however, and these may well be due in part to the different methods adopted or to differences in the position of the samples in such a critical area. Others are likely to be due to genuine differences in the conditions from year to year, and it is significant that using the same methods on an experimental record along a similar stretch of water in 1933 (mentioned on p. 71) we should have found rather different results. The main features of the phytoplankton populations for May, 1933, and May, 1939, are shown in Text-fig. 7. As we have just seen, *Rhizosolenia semispina* was widespread in May, 1939, but much more limited in 1933 ; the total Hyalochaetes were the scarcer in 1939 and the Phaeocerids in 1933 ; *Thx. longissima* was much more abundant in 1933, whilst the Dinoflagellates were mainly away from the coast in 1933 instead of in the coastal waters, as in 1939 (*C. fusus* still being the commonest species) ; in addition the Nitzschia spp. (including large numbers of *N. seriata*) were much more plentiful in 1933. In a number of these points there appears to be more resemblance between the 1933 record and the *fourth* of the present series, *i. e.* that taken early in July, and it may be that development in the present year was a little later. Whilst we can say little more about this in detail, it seems clear that whilst there can be such differences between records taken by the same means in different years and (as the present results have just shown) between consecutive records in the same year, much of the evidence from isolated cruises may be misleading. The North Sea data have shown clearly (*cf.* earlier ‘ Bulletins ’) that it is necessary to have regular records taken at time intervals as short as possible over several years before the trends in any area can be understood, and the present results show how necessary this will be in the Faeroe-Shetland area.



TEXT-FIG 7.—Showing the broad changes in abundance of ten phytoplankton organisms block by block along the Faeroe-Shetland line in May, 1933 (black), and May, 1939 (hatched). The symbols • (1933) and – (1939) denote the absence of an organism from the block concerned.

These traverses have amply borne out Gran's finding (1915) that the phytoplankton of this region developed much later than that in the North Sea, just as in the North Sea itself the phytoplankton of the north-west was later than elsewhere (*cf.* Lucas, 1941, for example). At a time when appreciable patches of diatoms were still present here, the Dinoflagellates had been typical over most parts of the North Sea for one or two months. In comparison with the records of the International Council during 1902–08 we must note the absence of *Cerataulina Bergonii* and *Asterionella japonica*, together with the scarcity of *Ceratium longipes* and *Rhizosolenia Shrubsolei* in our samples, whilst *Chaetoceros decipiens* seems to have been scarcer west of the Faeroes than they found it (see Ostenfeld, 1931). We have already commented upon the local scarcity of some of these in comparison with our findings at similar times in the neighbouring North Sea.

It is unfortunate that there should be so little published data regarding the zooplankton for effective comparison but, with the exception of the International Council's data, these seem to be limited to the generalized remarks of Paulsen (1909), Hentchel (1936) and (for the Chaetognatha) Fraser (1937 and 1939).[1] Of Paulsen's data we can say that he found most of the forms recorded by us in these waters, but that it is impossible to compare the details either of time or spatial distribution ; Hentschel, however, has some more precise information. After finding a very thin plankton in February (particularly off Faeroe), he found a much denser one in March, mainly between Faeroe and Shetland. Certain forms, such as the larvae of bottom animals, adult Calanus and Oithona he records as most abundant over the Bank and in the coastal zone, whilst the nauplii of Calanus were definitely most abundant near Faeroe only. Although the times are different, this may be compared with our findings that Calanus was most abundant near the Faeroe Bank and the mainland, whilst the younger stages were at first commoner just to the west of the Bank than anywhere else. In contrast with the generalized findings of the International Council for this area (Ostenfeld, 1931), we should note that we found no *Calanus hyperboreus* in these waters and little Pseudocalanus between Faeroe and the mainland, whilst Acartia and Limacina seem to have been relatively more abundant than one might have expected. In particular there are some discrepancies between their findings for Thysanöessa spp. and ours (Kramp, 1913, pp. 544 *et seq.*), but whilst on the whole the conclusions would appear to be contradictory for these two species, we must remember that our samples are taken only from a depth of ten metres, and may well be expected to give different results with forms such as the Euphausiacians, which are often very low in the water. Comparison between our data for the Chaetognatha and Fraser's has been made on p. 82 ; on the whole they are in agreement.

One other point may be mentioned here. On p. 73 we referred to the possible use of continuous recording for the purposes of detailed correlation between different constituents of the community. An aspect of this has already been mentioned when the various organisms were related to the four main sections of the route (coast, channel, Bank and deep water). In so far as such spatial relationships were well determined, so far is it possible to see interrelationships between the organisms themselves, although how far these are likely to be biological or physical (and how far it is safe to distinguish between these) is a matter for debate. More detailed consideration, however, of the associations shown in Text-figs. 6 and 7 will provide other correlations between the animals and the plants. The inverse relationships between the Euphausiacians have already been mentioned, as well as those between the various adults and their younger stages. A similar but not so marked inverse distribution applied to the older and the younger Calanus. As we have observed before, there was a general inverse correlation between *Rhizosolenia semispina* and *R. alata*, as well as between *Chaetoceros decipiens* and the other Hyalochaetes, both in time and space. Other, and more subtle, correlations can be found here and elsewhere in the continuous records, and will be discussed in later work. The method of illustration adopted here—showing at once the varying numbers at any time, the associations in space and the successions in time—may serve to introduce some of the possibilities in the work. In principle (and from the qualitative aspect) the phytoplankton data should be as productive as the zooplankton but, owing to the small size of the former, it is likely that the only precise quantitative results will be obtained from the larger zooplankton forms which are caught more representatively.

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[1] It is hoped that this will be partly remedied when the interesting information can be published which was outlined by Dr. J. H. Fraser (of the Fishery Division, Scottish Home Department) at a meeting of the Challenger Society in 1936, and at the Dundee meeting of the British Association in 1939.

The various changes in community have particular interest in view of the significant position which these records occupy, lying as they do between the definitive Atlantic water and the more northern waters, and adjacent to the North Sea. Owing to the onset of the war the relevant hydrological data has not been published and so the necessary correlations cannot be made now ; in their absence it is only possible to make the briefest comments on the distribution in relation to water movements. Elsewhere (Lucas, 1940) comment has been made on the difficulty of interpreting water movements from the changing shape and position of patches on a single line. Certain deductions can be made, however, within limits. Of the four sections of the route mentioned on p. 84, the coastal one has almost without exception maintained a separate plankton which has developed generally in a manner distinct from the others. This appears to correspond to the coastal zone found here by Fraser (1939), but at this depth our results suggest that its plankton is more distinct from that of the other waters than he found it. Its Calanus population was separated from that to the west of it and lasted longer, giving way to dominant Limacina. In particular, *Sagitta elegans* only occurred here, except for the one occasion when it appeared over the Faeroe Bank ; this exception is itself interesting, since Fraser recorded it as " absent in the Faeroe Channel " and " fairly common close around the Faeroe Islands." We have already commented upon the earlier diatom crops in both of these areas, but whereas the coastal zone was well defined and only slightly encroached upon as the season developed (perhaps decreasing in width by some twenty miles), the Bank region suggests greater and varying admixture with forms also found in the waters to either side of it. Thus some more or less " oceanic " forms, such as the Doliolids, extended at times over this part of the Bank, although others of them, such as Clione and the Chaetognatha, were practically restricted to the region of the deeper waters, whilst *Rhizosolenia alata* is the only form usually found over the deeper water which could be said to have extended over to the coastal zone.

It may be considered that such a distribution fits in well with the generalized picture drawn by Fraser (1939, and also in a paper read before Section D at the British Association Meeting in Dundee, 1939) and by Russell (1939). With these in mind the variations shown from record to record may be of value for interpreting the changing position of the different water masses in this region. The first record showed a very thin plankton, suggesting on the whole winter conditions over the part of the line recorded, whilst the appearance of *Metridia longa* in the second record may denote an area of arctic influence (perhaps still revealed in these surface waters by the Eukrohnia and *Sagitta maxima* found at the western end of the third record). Meanwhile the general distribution of Calanus and the phytoplankton then (May) suggested more temperate conditions over the greater part of the line, giving place in July to a plankton of warmer Atlantic forms, such as Doliolum and perhaps Tomopteris. This may even have been anticipated in May in a localized western region (adjacent to the arctic forms, and perhaps having arisen with them from deeper waters), denoted by *Sagitta serratodentata* and the dinoflagellates, the latter of which spread eastwards in July until in August they were over most of the line other than the coastal band. This suggested sequence (implying a sequence of water masses flowing across the line), if confirmed by other (*e. g.* hydrological) evidence, would not be improbable. More debatable points could only be cleared up by a longer period of observations. Such a point concerns the exact interpretation of the events in August. We see that the Doliolids decreased, whilst the numbers of Acartia and Temora increased. On the other hand, Tomopteris and Themisto increased, whilst Rhincalanus appeared for the first time. It is important to know how far these changes denote an increase or a decrease of the Atlantic conditions, or whether they were due to other factors.

The evidence from the present results alone will not clear up these points, but it is hoped that the tentative suggestions and the general picture so far available will serve to indicate the possibilities of more comprehensive work in this region as soon as oceanographical investigations are again possible. From the results of continuous records for a number of years it should be possible to obtain a better idea of the main features of the annual plankton cycle, of the kinds of differences which may be expected from year to year and, by comparison with results from the adjacent North Sea waters, to relate these constant features and the variations to similar features there. It is likely that some of the differences between the present data and those of other workers may be due to annual differences in the conditions of plankton growth, or the varying influence of different water masses.

It is possible that the year 1935, as judged by Hentschel's results, was a year of earlier plankton development than, say, 1934, when Nielsen took his early spring samples, or than 1939 ; it is also possible that 1933 was an " earlier " year than 1939. Similarly the variations in the number, spatial distribution and time of occurrence of the patches of Doliolids (or salps, which might appear in other years) might have significance in assessing the strength of the Atlantic influence in relation to trends in the North Sea. In view of the conformation of the sea bottom it is likely that the extent of the " coastal " zone is about normal, yet there may well be variations in the encroachment of the surrounding waters upon this strip. In any case, as Fraser has suggested, at times (though probably not in 1939, with the exception of Limacina) this may be an area of prolific production having significance for the commercial fisheries. Such variations might well repay further study. In order, however, to make such records more effective it would be desirable in any further survey to have data as far west as Iceland on this line together, it possible, with another line between Iceland and Bergen. Thereby more effective connection between the two waters might be established, and a better idea obtained of the interactions between the Atlantic influence, on the one hand, and arctic and coastal influences on the other.

SUMMARY.

1. From April to August in 1939 six Continuous Plankton Records were obtained on a line running from Sule Skerry for 300 miles towards Reykjavik, crossing the southern extrance to the Faeroe-Shetland Channel and out beyond the edge of the Faeroe Bank.

2. The individual distributions of the principle phytoplankton and zooplankton species are shown record by record, and are briefly related to the data of earlier workers and to comparable results in the neighbouring North Sea.

3. For a number of these species the data are rearranged in order of appearance and grouped so that their spatial and temporal distributions can be correlated. Associations between the different organisms themselves, and with the depths of water, are discussed.

4. Attention is drawn to the possibilities of further and more extended work in this area. The present data suggest that useful information might be obtained, *via* the various " indicator " species, concerning the influence of Atlantic water in this area and, in turn, on the neighbouring waters of the North Sea.

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CONTINUOUS PLANKTON RECORDS:

THE COPEPODA IN THE NORTH SEA, 1938–1939

BY

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INTRODUCTION, METHODS AND ARRANGEMENT OF THE DATA.

The Copepoda taken in the southern North Sea from 1932 to 1937 are described in ' Bulletin ' No. 4 (Rae and Fraser, 1941), together with the Recorder sampling method, the technique of analysis and the known limitations of both. This report concerns 1938–39, and a knowledge of the previous one will be assumed. In 1938 the Recorder survey was extended to include the whole North Sea by adding six new lines to those of 1937. These ran from Leith to Hamburg, to Copenhagen and to Lerwick, from the Pentland Firth to Hamburg and to Bergen and from Hull to Christiansand. This last line was discontinued after seven months and was replaced by a line running from Pentland Firth towards Iceland, which has been separately reported in 'Bulletin' No. 10 (Lucas, Marshall and Rees, 1942). The value of this extension has been discussed in ' Bulletin ' No. 7 (Hardy, 1941), which gives exact descriptions of the new lines and details of each record taken.

Work at sea had to be suspended on the outbreak of war after only 20 months. The object of this report is to outline the distribution of the Copepoda during those 20 months, to compare it with the more restricted data of the previous six years and, by considering it together with other work, particularly that of the International Council between 1902 and 1908, to draw a more detailed picture of the seasonal distribution and origin of the copepod population in the North Sea. It is hoped that this will provide a basis on which to plan future Recorder surveys, and at the same time provide a standard for comparison in later years.

Those records analysed before September, 1938, were treated in essentially the same manner as that adopted towards the end of the earlier survey (Rae and Fraser, 1941, p. 176). First the silk roll was cut up into blocks representing ten miles of sea sampled, a known fraction of each (approximately 1/20) was traversed with a microscope and all the copepods on it counted and placed in a category " Total Copepoda." When the plankton had been scraped from the silk it was re-examined until 100 individuals had been identified (or classed as unidentifiable). In samples containing less than 100 copepods, at least half of those present were examined. The total estimated on the silk was divided into the various species on the basis of the proportions found in the scraped material.

From September, 1938, onwards specific identifications were made at the same time as the estimation of the total, while the plankton was still on the silk. This was made possible by modifications to the apparatus (' Bulletin ' No. 1, Hardy, 1939), and because by this time it was practicable to analyse the rolls while they were still in a comparatively fresh condition. It then appeared wiser to examine a larger proportion of the silk when only a few copepods were present, while on the other hand it seemed both impracticable and unnecessary to spend the time required to identify specifically 1/20th of the individuals in the more abundant samples. An arbitrary scheme was adopted as a compromise, in which 3/40ths of the silk was traversed when the total number was of the order of 1300 or less, 1/20th when it was between 1300 and 2000, and 1/40th when it was larger than this. When more than 4000 were present, however, although 1/40th was traversed to give an estimate of the total, its constituents were based on 100 individuals identified, which were selected at random from the whole sample on the silk.[1]

As in the earlier work the larger forms such as Calanus, Labidocera, Anomalocera, Candacia, Euchaeta, Metridia and Rhincalanus usually occurred in numbers too low to be estimated adequately by sub-sampling technique. These were counted with the naked eye except when they were very abundant, and then a confirmatory estimate was made with the microscope.

The reasons for combining some species into conveniently recognizable categories (*i.e.* Acartia spp., Oithona spp. and the Pseudocalanus group) were discussed in ' Bulletin ' No. 4 (Rae and Fraser, 1941, p. 198). It was plain that, in the first place, the time spent on a complete specific identification would have been disproportionately large compared with the extra information gained. Secondly, had an attempt been made to determine all species, the far higher proportion of unidentifiable individuals would not have been a fair selection of the whole, as certain of the species which we had grouped are much more easily crushed beyond specific recognition, so that too low an estimate of their relative abundance would have been obtained. By adopting only the categories and species listed below very few were unidentifiable ; even in the least satisfactory samples these did not exceed 5% of the total, and were comprised almost entirely of young stages.

The recommendations of Gran, Hentschel and Russell (1936, p. 19) were again followed in identification, and some species not recorded in the earlier report (Rae and Fraser, 1941) were taken in the new area. As before, the identifications were based on G. O. Sars' (1903) ' Crustacea of Norway,' but as some species have been renamed more recently, the alternative names are added in the list given below :

Calanus finmarchicus[2] (Gunnerus).
Calanus hyperboreus Krøyer.
Rhincalanus nasutus Giesbrecht.
Paracalanus parvus (Claus).
Pseudocalanus elongatus Boeck = *P. minutus* (Krøyer) } Combined.
Microcalanus pusillus (G. O. Sars)
Euchaeta norvegica Boeck = *Paraeuchaeta norvegica* (Boeck).
Centropages typicus Krøyer.
Centropages hamatus (Lilljeborg).
Isias clavipes Boeck.
Temora longicornis (O. F. Müller).
Metridia lucens Boeck.
Candacia armata Boeck.
Anomalocera patersoni Templeton.

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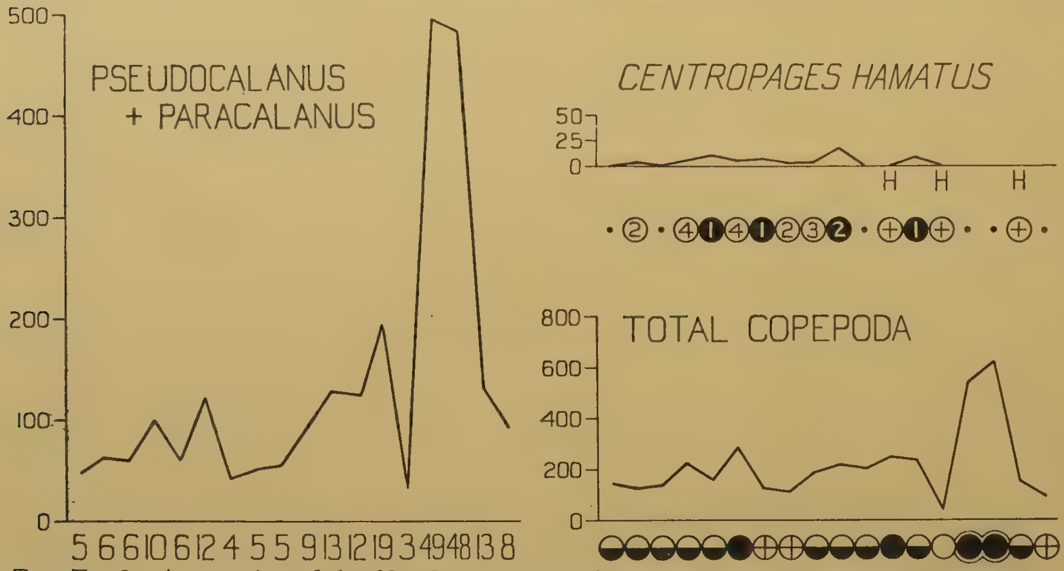
[1] This change in method introduced one minor inconsistency. In the earlier system a larger proportion of the individuals in a sparse sample were examined, and so the possibility of an uncommon form being seen and recorded as present was greater.

[2] *C. helgolandicus* was not differentiated (*cf.* With, 1915).

Labidocera wollastoni (Lubbock).
Parapontella brevicornis (Lubbock).
Acartia spp.
Oithona spp.
Corycaeus anglicus Lubbock.
Other Cyclopoidea.
Harpacticoidea.

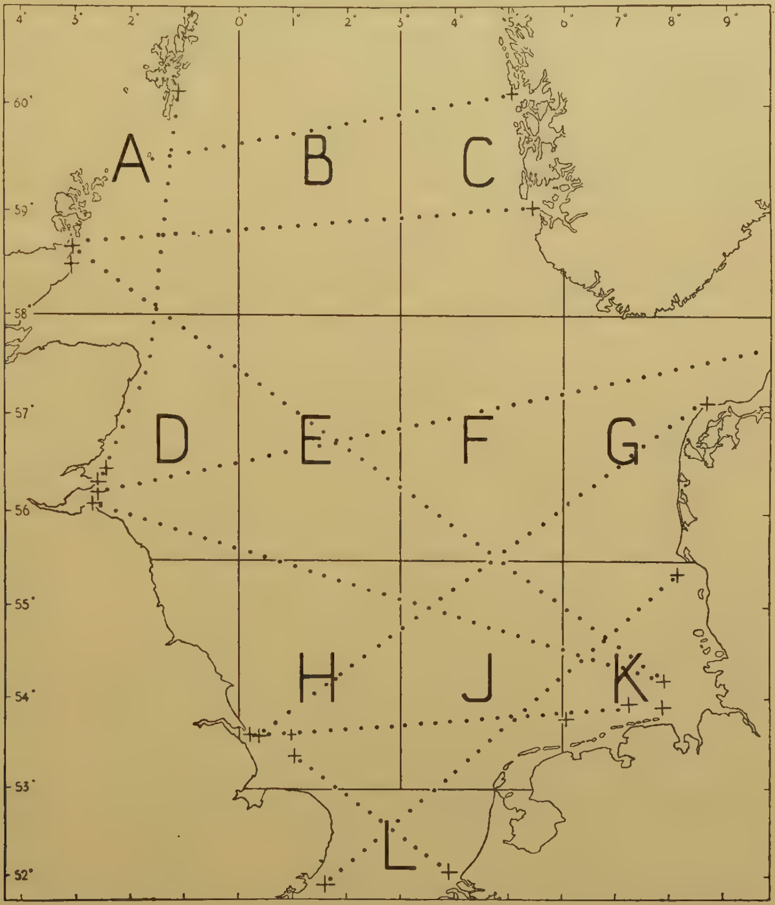
Details of all usable records for 1938–39 are shown on charts already published (Hardy, 1941). These charts differ in some ways from the series presented here for several reasons. Firstly, the majority of the records classed as of "qualitative value only" have been neglected. Secondly, when more than one record was taken in a month, usually only one was analysed, except on the Lerwick and Bergen lines, where two records a month was the schedule aimed at. Thirdly, there was usually an accumulation of copepods on the last two inches of silk, which seemed to be attributable to the hauling process, and so the last block was discarded.



Text-Fig. 1.—A comparison of the old and new methods of charting the varying quantities of Copepoda along the Recorder lines: immediately below each of the three examples of the graphical method used in 'Bulletin' No. 4 is placed the equivalent set of numerals or symbols used in the present 'Bulletin.'

With the new intercrossing lines it became impracticable to continue the graphical method of presentation used for the 1932–37 data. In the monthly distribution charts a series of numbers or symbols representing the catch on each 10-mile block is used instead. The estimated numbers are given for Calanus, the Pseudocalanus group, Temora, Acartia, Centropages and Oithona, but symbols are used for the Total Copepoda and other forms. Text-fig. 1 gives examples of these methods of presentation in comparison with those of the 1932–37 report.

In addition to the charts showing the monthly distributions along the Recorder lines, a series of histograms has been prepared (Plates LXIII–LXV) to give a summarized picture of the relative abundance of the Total Copepoda and the commoner forms in the different areas during the 20 months period. The area



Text-fig. 2.—A chart showing the arbitrary sub-divisions of the North Sea used in computing the average monthly catches of Copepoda shown on Plates LXIII–LXV. The dots represent the centres of the " ten mile blocks " on the Recorder lines ; the small crosses mark the position of the lighthouses or lightships at the ends of each line.

covered by the survey is divided into arbitrary sub-areas, each covering 3° of Longitude and 2½° of Latitude. Text-fig. 2 shows these areas and the number of blocks which might have been sampled in each in a month if all records had been complete; they are labelled alphabetically from west to east and north to south. Then the average numbers of copepods per mile in each sub-area for each month are calculated and plotted as histograms. A separate histogram shows the fluctuation in the monthly average values for the *whole area.* In addition are given estimates of the average numbers in each sub-area for the whole 20 months' period; these are shown immediately below the reference letters indicating the different sub-areas.

These histograms are subject to a number of limitations. It is clear from Text-fig. 2 that, while sub-areas such as J and K can be adequately sampled in months with a high proportion of successful records, we cannot expect so fair an impression of the plankton in B or C from comparatively few observations on a single line. The Leith to Lerwick line was only taken for a part of the year and so may have a biasing effect in sub-areas A and D; it gives more observations there during the spring and summer when the plankton is most abundant, and so results in a disproportionately high value for the 20 month period. There are other limitations, such as the absence of records or part records in some months, sampling on alternative routes, and variations in the date of records, all of which make the averages not strictly comparable. Nevertheless, as generalizations, they form a convenient summary, and make clear a number of points which are not so readily seen from the monthly distribution charts. Further, we believe that if continued as a summary they will form a convenient index to the detailed data which will accumulate year by year. They will demonstrate the major trends at a glance, and the reader need only refer to detailed information in cases of doubt or particular interest. In earlier 'Bulletins' much space was devoted to describing the plankton distribution found in what may be considered as the first really detailed survey of the North Sea. In later 'Bulletins' more time will be spent in considering it in terms of its environment, and the pure description of its distribution may be restricted to such summarized form except in special cases.

It has been stressed before that, although the Recorder data can be compared within themselves to give a relative picture of plankton distribution in space and time, considerable care must be exercised before comparing them with those obtained by other methods. In fact it is doubtful whether, even if the Recorder catches were converted to copepods per unit volume of water, they would be strictly comparable with the more normal net samples. While the Recorder sample is small, the proportion of the catch identified and counted is large; the small sectional area of the Recorder aperture, $\frac{1}{2}$ inch square, may bias the ratio of large to small planktonts in the catch; when plankton is abundant the Recorder may be functioning near its upper catching limit and our highest figures may appear unduly low. These limitations and others that have been discussed in earlier 'Bulletins' (Hardy, 1939, p. 44) need not concern us so long as we consider only the broad changes and trends and minimize the significance of individual values. The changes and trends may fairly be compared with the conclusions drawn from other sources of information so long as exact numerical agreement is not expected. Bearing this in mind we have used as pictorial a manner as possible, and restricted reference to actual numbers to a minimum. Nevertheless scales are included in each diagram which show the numbers caught per mile of tow or, in some cases, per ten miles of tow.

Apologies are due to the reader for the inconvenient arrangement of the lithographed plates at the end of this report. Plates LXXXV–LXXXVIII are intended for use with a lens, but even so the numbers are not distinct in all cases. Further, it is frequently necessary to turn from plate to plate to follow the varying distribution of any one species through the period, whilst it would be more convenient if the charts for each organism were on successive Plates. In mitigation we explain that the arrangement was forced upon us by the war. The charts were ready in 1940, but the text was incomplete when the authors entered the Forces. The future seemed insecure, and it was thought best to take advantage of the very limited quota of paper allowed to print the data then available. It was only possible to print all the copepod data if they were much compressed.

Distribution of the Copepoda.

Total Copepoda. (Plates LXIII, LXVI and LXVII.)

Again the group " Total Copepoda " is considered as a whole. The Copepoda form a large proportion of the smaller zooplankton throughout the year and are an important link in the food chain. They are probably the largest group consuming diatoms in the North Sea, and in their turn provide a major part of the diet of young fish. We think that in attempting to understand how long-term changes in the physical and biological conditions may affect the commercial fisheries, which is one of the objects of this survey, it will be useful to have readily available a picture of the fluctuations in the overall copepod population year by year in spite of the known ecological differences between its constituents. Clearly in a detailed consideration one would have to allow for the variation in the sizes of the constituent species. It would require many individuals of the smaller species, such as Oithona, to provide the equivalent mass to a single Calanus. No effort has been made towards such adjustments at this stage.

A summary of the distribution of the Total Copepoda in time is shown on Plate LXIII. Taking the whole area there was little difference in the population in the two years. In 1938 the maximum catch was taken in July, while in 1939 an equivalent number was recorded in May, but thereafter there was a decrease until the survey closed in August. There were, however, considerable differences between the sub-areas ; in squares A and D there were more copepods in the summer of 1938 than 1939, while further south, in E and H, the reverse was the case, as it was most markedly off the mouth of the Skaggerak in square G. Again, it appears that numerically the difference between summer and winter was less marked in the east than the west, and least in the extreme south, where copepods were relatively scarce throughout the year. The diagram also shows that in the south the sparse winter population was more successful in the early months of 1938 than in late 1938 and early 1939.

Plates LXVI and LXVII show a more detailed picture of the monthly distribution. The winter charts for January, February and March in both years, together with that for December, 1938, are in accordance with the more restricted data available in 1932–37 ; the larger numbers were accumulated in the continental coastal waters, particularly in the Heligoland Bight. It was then concluded (Rae and Fraser, 1941) that the increase in the spring population was due to some influence moving southwards across the Dogger Bank, since the first indications of it were usually found over the Dogger Bank and maximum numbers were found in the south later than in the north. The wider picture in 1938–39 gives a different impression. There appear to be several centres of development leading to a general increase over the area, which is certainly not solely the result of larger numbers being carried into the area by more productive northern waters. Unfortunately the information for March, 1938, was scanty, but the few samples available fit in with the general winter distribution expected. By April, however, higher numbers were found over the Dogger Bank and off the north Danish coast. This is even more apparent from the comparison of the March and April charts for 1939. In neither year was there any sign of large numbers of copepods appearing off the Scottish coast until May. Later in the year the Moray Firth–Shetland region, which comes more directly under the influence of higher salinity " Atlantic Water," may support a denser population than the rest of the North Sea, as can be seen on the July charts ; but in May and June of both years the copepods were already well established to the south, in the centre of the North Sea. There appear to be, in fact, at least four distinct regions in which the spring increase may occur :

(*a*) off the mouth of the Skaggerak (April, 1938, and April, 1939),
(*b*) off the north-eastern Scottish coast (May to July, 1938 and 1939),
(*c*) the extreme south (May, 1938, and April, 1939),
(*d*) over the Dogger Bank and to the north-west of it (May, 1938, and April–May, 1939).

Before considering the possible origin of these accumulations of copepods, it will be well to determine whether they are increases of the whole population or only of certain communities or types.

Each species or group of species will be discussed briefly in turn. In the main, the diagrams contain all the available information and speak for themselves, so that description can be kept to a minimum. When mentioning earlier ideas regarding the normal habitat or idiosyncrasies of any form, particular attention will be paid to the results of the International Council's investigations between 1902 and 1908 as summarized in the ' Bulletin Trimestriel ' (Farran, 1910 and 1911 ; Scott, 1911 ; and Ostenfeld, 1931), while many other observations will be neglected. This is intentional. In the first place the ' Bulletin Trimestriel,' although in some instances far from definite in its conclusions, does provide a standard method of comment on all but one of the species we discuss. It is based on a long series of observations over a wide area which includes the North Sea and the waters adjoining it, whereas other work has inevitably been more restricted. Secondly, it has proved far easier to compare with such a standard than to attempt to collate the many other isolated series of observations by making allowances in each case for the different methods of collection, computation and presentation of results. Further, we believe that it is necessary, in order to smooth out the very patchy distribution that occurs in space at any one time, either to take a large number of samples over a large area in a short time, as is done in our method, or alternatively to base one's observations over a very long period as was possible for Farran, Scott and Ostenfeld.

Calanus finmarchicus. (Plates LXXIV–LXXVII and LXXXV.)

The importance of *Calanus finmarchicus* in the economy of the sea has been established by many workers. It has often been selected from the Copepoda as the species for special study, and compared with other species much is known about its seasonal distribution, life-history and behaviour. Such available knowledge facilitates further work, and this fact, together with the known Calanus-Herring relationship (Hardy, Lucas, Henderson and Fraser, 1936), has encouraged us to select it for special consideration. A separate report by Mr. Rees (in preparation) contains the findings derived from the Recorder material for the whole period, 1932–1939. However, a certain amount of information is included here for comparison with the other species.

In the method of analysis (p. 97) the larger specimens were counted with the naked eye and recorded as " large Calanus," whereas the smaller copepodite stages were estimated by a microscope traverse. In presenting the results adults and stage V are added together and given as numbers per 10 mile block, while younger specimens are lumped together and shown as numbers per mile.

Adults and stage V (Plate LXXXV) were present over most of the area even in the less productive winter months. This is in keeping with the accepted view (Nicholls, 1933; Gibbons, 1933 and 1936; and others) that a residual population survives throughout the winter in the Vth copepodite stage. It is interesting, however, to note its persistence in winter in the extreme south in an area which does not appear to be very favourable for it at other times of the year when compared with the north and centre of the North Sea. In the summer months (Plates LXXVI and LXXVII) the population was patchy but, in the main, the bulk was towards the north; except for restricted patches off the mouth of the Humber few were found south of a line due east from Flamborough Head. The most productive areas were those off Orkney and Shetland and southwards, and off the mouth of the Skaggerak and northwards along the Norwegian coast; in fact, in this latter region, which is included in square C in the summarized analysis, Calanus constituted half the total copepod population over the period.

The distribution of the younger stages (Plates LXXIV, LXXV and LXXXV) was similar. In January and February, 1938, and from October, 1938, to February, 1939, they were scarce over the area, while during the spring and summer months they were common and their distribution agrees well with that of the older stages. The relationship in space and time between the younger and older stages will be discussed fully by Mr. Rees, in a later Bulletin.

Calanus hyperboreus. (Plates LXX and LXXI.)

C. hyperboreus was rarely included in the Recorder catches, but its occurrence was well defined in space and time. It appeared off the Norwegian coast in March, 1939, persisted in April and May, and was also present in the mouth of the Skaggerak in April. Plate LXX shows that this region was poorly sampled in 1938, but this species was not found in the comparable samples in April and May. It is interesting that it occurred in association with *Euchaeta norvegica.*

Farran (1911) described *C. hyperboreus* as an arctic form whose distribution followed the course of the East Icelandic Polar current, and stated that its occurrence in abundance was restricted to water of this origin. It was also found regularly during 1902–1908 in small numbers over the southern North Sea and off the south coast of Norway, and was common in the Skaggerak.

More recently, however, Sømme (1934) has made a comprehensive study of the biology of this species with particular reference to its behaviour and distribution in the Lofoten area, where he found a persistent stock in the deep stagnant layers. There was a single breeding period early in the year, and at about the time of spawning there was a mass vertical migration of females to the upper layers, which led to their spreading off shore and subsequent dispersal in the prevailing currents. This mass migration took place in February and March and was completed by mid-April. Further south, off Møre, Ruud (1929) found a similar seasonal vertical distribution. It seems likely that *C. hyperboreus* behaves in the same manner along the whole coast line of Norway wherever suitable deep water conditions exist for its normal habitat. The restriction of its appearance in the Recorder samples at 10 metres to March, April and May agrees well with Sømme's timing of the vertical migration, and its apparent absence at other times of the year is compatible both with the idea that it is essentially a deep water form, and with the findings of With (1915), from the East Greenland Expedition material, that it was one of the few copepods that did not exhibit a diurnal migration into the upper layers.

Rhincalanus nasutus. (Plate LXXI.)

R. nasutus, which is undoubtedly an Atlantic form, was found only once during the survey, midway between Pentland Firth and Bergen in January, 1939.

Pseudocalanus elongatus, Paracalanus parvus and Microcalanus pusillus. (Plates LXIV, LXXVIII, LXXIX and LXXXVI.)

Throughout this report these three species are considered as a single group which for convenience is termed the " Pseudocalanus group." There is no doubt that if sufficient time is spent and the material is fresh, they can be separated in Recorder samples, as in fact was often done. The impression then gained was that Pseudocalanus was far and away the most abundant of the three, though Paracalanus was at times commoner in the extreme south, especially in the autumn and winter, and Microcalanus sometimes occurred on the more northern records.

The Pseudocalanus group was clearly predominant in the North Sea during the period, as in fact it was in the southern area during the previous five years. Over the whole area it constituted 46% of the Copepoda caught, but it formed a bigger part in the south than in the north, varying with latitude from two-thirds to one-third. Plate LXIV shows its summarized distribution. It was more evenly spread in both space and time than the other forms, and reflects fairly closely the distribution of the " Total Copepoda " already discussed. In detail, Plates LXXVIII, LXXIX and LXXXVI show that it was well represented in the main copepod concentrations.

Euchaeta norvegica. (Plates LXX and LXXI.)

E. norvegica has been described as an inhabitant of the North Atlantic and Polar Oceans (Farran, 1911), and also as characteristic of the deeper layers of the Norwegian Sea (the " Euchaeta Region " of Gran, 1902). Sars (1903) described it as being common in the deeper waters off the west coast of Norway. Ruud (1929) again stressed its deep water habitat, and found in the Møre area that it had a similar distribution to *C. hyperboreus*. March was the only month in which he found it near the surface, when spent females appeared in the upper 50 metres, and as April, 1939, was the month in which by far the largest numbers were taken during our survey, it may be that it carries out the same type of mass migration towards the surface as *C. hyperboreus*. However, in our catches it was not so restricted in time as *C. hyperboreus*, being taken off the Norwegian Coast in July, August, October, November and December, 1938, and March, April, May, July and August, 1939, and off the Skaggerak in January and December, 1938. It is of note that, with one exception, July, 1938, all those taken off the Norwegian coast were caught over the deep side of the 100 fathom contour, and those from the Skaggerak were over or near the deep channel which is in the main about 75 fathoms deep. Again with the same exception, they were all taken during the night, but clearly the spatial restriction found is not purely the result of diurnal migration, as the species was consistently absent from night samples elsewhere in the area.

Centropages typicus. (Plates LXV, LXXXII, LXXXIII and LXXXVII.)

Particular attention was paid to *C. typicus* in ' Bulletin ' No. 4. This species was one of the few which showed an autumn maximum in the southern part of our area. There were variations between the autumns and winters of 1932–1937, but on the three southern lines then sampled it was evenly spread in or about August, increased in numbers in the following months and, while increasing, conformed to the general winter distribution of the copepod population (i.e. a concentration off the Dutch coast and in the Heligoland Bight, with an even distribution across the southern North Sea on the Hull to Copenhagen traverses). Such a distribution appeared interesting in view of the reports of the International Council on the species. Scott (1911) stated that it was " a true Atlantic form," but was " more common inshore and in limited areas." However, Ostenfeld (1931) in his summary was more definite about the area of interest to us; he wrote that it " seems to be most common in the western part of the English Channel and in the Faroe-Shetland and east of it to the Skaggerak, thus rather rare in the southern and central North Sea. In the Shetland region maximum in August, November, in the English Channel common the whole year round." Russell (1936) selected it from the species described by the International Council as being typical of his category: " Atlantic oceanic, existing all the year round under neritic conditions," as opposed to *C. hamatus*, which he used as an example of the " neritic " forms. Clearly, the former description was not compatible with our finding that *C. typicus* comprised a considerable part of the winter population in the Southern Bight, and the question of its origin arose. There were obvious alternatives. Firstly, the species might be more successful indigenously than previously supposed or, secondly, it might have received unusually strong recruitment from a habitat either in the north or in the Channel where it was more successful. The restricted area of our results prevented any detailed consideration on this point, though it was hoped that information from the extended area would help to resolve it. But, as will be seen from Plate LXV, the autumn of 1938 was particularly unsuited to this purpose. In that one autumn only, of the seven we have investigated, did *C. typicus* fail to establish itself in squares K and L, and in no part of the southern North Sea did it persist over the winter months in any appreciable numbers.

However, by reference to the charts on Plates LXXXII, LXXXIII and LXXXVII it is possible to trace tentatively the movements of *C. typicus* through one complete year. The autumn of 1937 (Plate CXVIII, 'Bulletin' No. 4), showed it as scattered in low numbers over the centre of the area and accumulated in larger numbers in the Heligoland Bight. January, 1938, was poorly sampled, but the chart for February shows that this population had persisted with a similar distribution. Numbers had decreased by April, and remained low with spasmodic occurrences in May. By June, however, although numbers remained low over the bulk of the area, larger numbers were found in the north-west off the Shetlands, and this had become more marked by July. During August and September the concentration in the north-west was maintained, but the species extended progressively further south, until it became established all over the area except in the extreme south. In October this successful population in the north-west had disappeared, but high numbers remained in the east and central North Sea, decreasing through November to a very low level in December.

As we shall see later, such a sequence runs parallel to that found for *Candacia armata* and *Metridia lucens*, which are indubitably indicators of the southward movement of the mixed water from the north of Scotland, and in view of Ostenfeld's remarks (see above), one might be tempted to include *C. typicus* in the same category as those two northern forms, and so consider it as a fair indicator of "Atlantic influence " in the North Sea. However, our results for 1939 do not support such a belief because, although less successful than in the previous year, *C. typicus* established itself in the central North Sea without any apparent recruitment from the north-west. There were a few observations of its presence in the mouth of the Skaggerak and scattered over the northern half of the area in March, April and May, but by June it was well represented on the Leith to Copenhagen route, and although increasing generally, remained centred about this line when the survey ended in August. There was no indication at any time in 1939 of dense concentrations in the north-west comparable with those found in the autumn of 1938.

Centropages hamatus. (Plates LXV, LXXXII, LXXXIII and LXXXVII.)

Scott (1911), in summing up earlier work and the results of the International surveys, infers that *C. hamatus* is common in the North Sea and English Channel, but becomes progressively scarcer in regions more typical of oceanic conditions. Russell was more definite in his interpretation of the International Council results when he (1935) used the distribution of *C. hamatus* to illustrate the boundaries of his " *Sagitta setosa* water " and when he (1936) selected it as a typical " neritic " form.

We found in the southern half of the North Sea from 1932 to 1937 that the distribution of *C. hamatus* was similar to that of the main summer forms, i.e. Pseudocalanus, *T. longicornis* and Acartia spp., and the information available from the extended area in 1938 and 1939 confirms this. The species was never abundant when compared with the forms described above, but nevertheless it had a well-marked maximum in the spring or early summer. Plate LXV shows a summarized distribution, and we see that it was present all over the area except in the north-east, square C, in the summer of both years. It was particularly successful in the north-west in water where the Sagitta population was exclusively *S. elegans* (' Bulletin ' No. 13, Marshall, 1947), and also off the Humber, square H. However, by following the detailed distribution shown on the maps on Plates LXXXII, LXXXIII and LXXXVII, it can be seen that the summer increase had a southern tendency which was quite unlike that for *C. typicus*.

Isias clavipes. (Plates LXXI and LXXII.)

As in the earlier years, 1932–1937, *I. clavipes* showed a late summer maximum in 1938. It was present in a few samples in June and July, became more generally spread in August, and remained well represented from the mouth of the Humber across the Dogger Bank in September and October. The year 1939 provided either an unusually late season for *I. clavipes* or a particularly bad one, as it had only been found in two blocks off Humber by the end of August. The August–September maximum in 1938 confirms the results in the ' Bulletin Trimestriel ' (Farran, 1911). His results, however, showed the species as being more numerous in the channel and on the western side of the North Sea as far north as latitude 55° N., while all our results have consistently shown a preference for the Dogger

Bank region. We see in 1938 that it was restricted to the central North Sea and singularly absent in the north and extreme south of our area. In 1938 it tended to a more northern distribution than in the previous years, as not only did it fail to establish itself on the Hull to Rotterdam line, but it was generally more abundant over the Dogger Bank than on the Hull to Bremen line, whereas between 1932 and 1937 the reverse was the case.

Temora longicornis. (Plates LXIV, LXXX, LXXXI, and LXXXVI.)

T. longicornis represented 12% of the total catch during the survey, and so can be considered numerically as one of the more important members of the copepod population. It is clear from Plate LXIV that all over the area it enjoyed a much shorter season of success than the Pseudocalanus group, generally being restricted to two or three months. In the main it was far less abundant than the Pseudocalanus group, but during its peak periods it was nearly as plentiful. Plates LXXX, LXXXI and LXXXVI show clearly how restricted and patchy its distribution was.

Again, the few *T. longicornis* taken in the winter months were concentrated in the Heligoland Bight. The first signs of the spring increase occurred in April or May, and it is of note that denser patches were found in the centre and south of the area in each year before similar numbers were found in the Orkney–Shetland area. The distribution in the months available for comparison in the two years suggests that there was a common pattern, but that success or failure varied in degree.

Metridia lucens. (Plates LXVIII and LXIX.)

M. lucens is an "Atlantic" form, which according to Farran (1910) was always abundant to the south and east of the Shetlands and in the Skaggerak. This latter community he believed to be isolated and dependent on particular local conditions.

In our earlier results ('Bulletin' No. 4) we found occasional specimens off the Humber during the autumns and winters, and it was then stated that, together with *Candacia armata*, *M. lucens* should prove a good indicator species of northern influence in the North Sea. The results for 1938 and 1939 bring out well the northern distribution of the species. Had there been data only from the southern half of the area as in 1932–1937, we should again have found *M. lucens* appearing off the Humber in the autumn and winter, *i.e.* October, 1938, and January and February, 1939, but we now have a fuller picture of its invasion and subsequent movement in the North Sea.

M. lucens was found off the north Danish coast in the winter of 1937 ('Bulletin' No. 4, Text-fig. 10), and as can be seen on Plate LXVIII, was well represented there and in a band stretching westward across the North Sea in January and February, 1938. It occurred with varying success all over the northern half of the area throughout the 20 month period, but nevertheless showed signs of the movements which one might expect for a northern form which was carried into the area. A relatively dense patch had developed in the Orkney–Shetland area by August, 1938, and it increased in September. Thereafter there appeared to be a progressive extension of its distribution to the south and to the east, culminating off the Humber in January, 1939, and in the mouth of the Skaggerak in December, 1938. By August, 1939, another patch was established in the north-west as though the sequence was restarting. If we consider the occurrence of reasonably high numbers off the Orkney–Shetland channel as being indicative of an invasion from the north, it is interesting to note that there were also signs of ingression of *M. lucens* in the spring of both years (see May, 1938, and April/May, 1939.)

Candacia armata. (Plates LXX and LXXI.)

In *C. armata* we have another typical " Atlantic " form. The results of the International Investigations (Scott, 1911) showed that it had a distribution similar to that we have come to expect for *Sagitta elegans* (Russell, 1939). It was then found in the western Channel and around the Shetlands, but was absent from the eastern end of the Channel and from the North Sea south of a line drawn from the Firth of Forth to the Skaggerak ; however, it was recorded occasionally in the Skaggerak and off the south-west coast of Norway. In our survey we found occasional specimens in the winters of 1932, 1933 and 1934 between the Humber and the Dogger Bank (' Bulletin ' No. 4, Text-fig. 10.)

Plates LXX and LXXI again show just the sequence in distribution that might be expected for such an exotic carried into the North Sea by the " Atlantic current " from some region to the north-west of our area. In January and February, 1938, *C. armata* occurred over the northern part of the area, and was taken in one sample as far south as the Humber. It was not found again until August, when it appeared in a patch restricted to the north-west, off the Shetlands. Thereafter it spread southwards and eastwards, reaching the Skaggerak by October and the Humber region in November. By November the numbers in the north-east were decreasing, and there were only scattered occurrences over the northern half of the area in December. From January until July, 1939, only few and scattered individuals were taken, but by August a well-defined patch had reappeared to the south-east of the Shetlands as in the previous year and probably the same sequence of events was restarting.

Had only the southern lines been sampled, as from 1932–1937, *C. armata* would still have been recorded as present off the Humber in November, 1938, and January, 1939, and even further south off the East Anglian coast in December, 1938. This would have agreed well with the months of occurrence in 1932, 1933 and 1934, and if the 20 months now under consideration are too short a period for us to suggest August to October as the season during which *C. armata* is carried into the North Sea, we can conclude with some confidence that it is in the winter months that it penetrates furthest south. This is also true for *M. lucens*.

Anomalocera patersoni. (Plates LXX and LXXI.)

The scarcity of *A. patersoni* in the Recorder material between 1932 and 1937 was fully discussed in 'Bulletin' No. 4 (p. 230). The International Council's findings[1] and those of other workers would have led us to expect it to be at least as abundant as *Labidocera wollastoni* and more widely spread in the area. Gran (1902), however, listed it with *Metridia lucens* under the heading "Temperirt-atlantisches, oceanisches Plankton-Element." Our earlier data showed it to be far less common than Labidocera, and the same was the case in 1938 and 1939. As explained in 'Bulletin' No. 4, it is thought that its pecularity of swarming at the extreme surface may account for its scarcity at the Recorder level of 10 metres.[2]

Plates LXX and LXXI show the time and place of catches during 1938 and 1939. Although many of the records were isolated it was often taken on a series of consecutive "ten-mile blocks," whilst in 1939 it was found in the same place on two successive records in August. When this happens, as in the case of *C. hyperboreus*, we feel that we can assume the existence of definite concentrations, and that it is not merely the random sampling of an evenly distributed but very scarce form. We can say then, with due reservation, that *A. patersoni* was *relatively abundant* off the Skaggerak in June, 1938, off the Forth in August, 1938, in the north-west in October, 1938, and in the north generally in August, 1939, and was scattered over the centre of the area during the summer months. Our results are in agreement with Scott (1911) in that it is a summer form.

Labidocera wollastoni. (Plates LXVIII and LXIX.)

L. wollastoni occurred as a summer and autumn form in 1938–1939 as it did between 1932–1937. Except for isolated instances in January–February and May, 1938, it was first taken in June, increased through July, and was abundant in August, September and October. In 1939 it appeared in June again off the Humber, increased in July, and was relatively dense by August, when the survey ended. Scott (1911) made little comment about this species except that it had the same seasonal distribution as *A. patersoni* in reaching its maximum in August or later, although in his Plate XXI it is shown as being well restricted to the southern North Sea and English Channel. However, he quotes Sars (1903), who considered it to be a true pelagic form usually occurring in the open ocean.

Our impression from the earlier Recorder results was that in our area Labidocera had a marked preference for the centre of the North Sea. During the period now under consideration it was only once taken north of the line from the Forth to the Skaggerak, and its centre of concentration appeared in both seasons to be about the Dogger Bank.

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[1] See Scott (1911), Plate XXI.

[2] Cheng (1941) produces contributory evidence which was not available for inclusion in 'Bulletin' No. 4. *A. patersoni* was found in the stomachs of herring feeding in the Shields area in 1932 (Savage, 1937), while it was almost entirely absent from samples taken between 7 and 10 metres with the Plankton Indicator at the same place and time. Cheng is disinclined to accept the suggestion that the bulk of Anomalocera swim above the 10-metre level because Russell (1927) showed it spreading to the deeper layers during the summer months.

Parapontella brevicornis. (Plates LXX and LXXI.)

P. brevicornis is a tychopelagic form which appears in the sub-surface plankton in the autumn and winter ('Bulletin' No. 4, p. 231). In 1938 it appeared in the southern North Sea in August, September and October, and in 1939 in March and August. This is in agreement with our earlier results and those of the International Investigations.

Acartia spp. (Plates LXV, LXXIII, LXXXIV and LXXXVII.)

It has proved impracticable to identify the species of Acartia during the routine analysis. Almost certainly the population in the area is a mixture of *A. longiremis* and *A. clausi*,[1] but we can give no idea of their relative abundance. This is unfortunate, because earlier work would suggest marked ecological differences between them which would be useful in considering the origin of the copepod communities found. The 'Bulletin Trimestriel' (Farran, 1910, pp. 75–79 and Plate X) describes *A. longiremis* as a "neritic species having its headquarters along the south and west coasts of Norway and in the Skaggerak and Baltic. It ranges in small numbers from the Arctic Ocean through the Norwegian Sea and North Sea to the English Channel." *A. clausi*, on the other hand, is "widely distributed in small numbers in the oceanic area of the N.W. Atlantic but finds its most abundant development in enclosed waters, such as the Irish Sea and English Channel, in the warmer months of the year. It is absent from waters of low salinity." Here, then, we have two forms, which, in the area covered by our survey, may be expected to have similar boundaries to the much used indicator species of Sagitta, *S. setosa* and *S. elegans* (Meek, 1928; Russell, 1935, 1939; Fraser, 1937, 1939), and it may be worth while returning to the data in the hope that a useful proportion can be identified in catches taken from areas where the origin of the plankton is in doubt.

The summarized information given on Plate LXV shows that Acartia was localized but, where present, was an important member of the population. It was markedly coastal, and except in the winter concentration in the Heligoland Bight was only abundant during the early summer. There were large numbers off the Scottish coast in the summer months of both 1938 and 1939, but there was a marked difference on the eastern side of the area between the two years. Whereas in 1939 it formed an important part of the total catch in squares F, G, J and K, from April to July in 1938, it was only found in any numbers in square K. The distribution charts show that it is essentially coastal.

Oithona spp. (Plates LXIII and LXXXVIII.)

The genus Oithona was omitted from our earlier results because it was known that an appreciable proportion of those caught were lost during the removal of the plankton for examination of the zooplankton. The change in technique in September, 1938, eliminated this difficulty, and so data are included in this report from then onwards. Three species were identified, *O. similis* Claus, *O. nana* Giesbrecht and *O. spinirostris* Claus, but they were not usually separated in analysis and the data are shown for the genus as a whole.

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[1] *A. bifilosa* and *A. discaudata* may also be included in rare cases

The September map shows what presumably was the remains of the previous summer stock arranged in a patchy manner in the centre of the area, with a northern concentration off the Orkney–Shetland channel. From October to the following April, except for scattered records of presence or low numbers, the genus was not taken. In May there were signs of an improvement in the central North Sea, giving rise to a comparatively dense centrally placed population which persisted until August, when a patch off the Scottish coast had reappeared.

Van Breemen (1903) found *O. similis* and *O. nana* to be mutually exclusive in the North Sea, and Farran (1911) in summarizing the results contained in the International Bulletins supported this view. Apparently *O. similis* is common in the western channel and in the North Sea north of 53°N., whereas *O. nana* occurs between these two boundaries. In the twelve months for which we have Recorder data Oithona hardly occurred in the above defined *O. nana* area, but during the summer months was common to the north of the southern boundary of *O. similis*. We believe that specific identification of our material, had it been complete, would have been in agreement with Van Breemen, because the impression gained was that specimens of *O. nana* were exceptional, and by far the majority of the catch comprised *O. similis*. *O. spinirostris* occurred in the north.

Corycaeus anglicus. (Plates LXXI and LXXII.)

From 1932–1937 *Corycaeus anglicus* was found to be a winter form in the southern part of the area, often showing a similar distribution in both time and space to *Centropages typicus*. It appeared in the autumn, and by mid-winter was concentrated in the Heligoland Bight and off the Dutch coast. It appears probable from the results now before us that its association with *Centropages typicus* resulted from the fact that both species thrived at the same season and, in common with most other forms present in the southern North Sea in the winter, were subject to some heaping effect against the continental coast. We can see that whereas *Centropages typicus* may have been carried southwards from the north where it was more abundant, *Corycaeus* was restricted to the south throughout the year, but nevertheless, as stated above (p. 106), the winter of 1938/39 was clearly an abnormal period for *Centropages typicus*.

The dense population found in the Heligoland Bight at the end of 1937 was still apparent in January and February, 1938, and *Corycaeus* for the first time since the institution of the Recorder survey persisted in low and scattered numbers throughout the spring and summer months. By September, 1938, it had reinstated itself in large numbers off the Danish coast and remained there in a strip of water off the continental coast until December, after which it declined, although it was recorded as present there in January, February and June.

DISCUSSION.

The Relative Abundance of the Constituent Forms.

In the preceding description the occurrence and distribution of each form has been discussed on its own merits, and little attention has been paid to the relative abundance of the constituents of the population. It is probably wiser to avoid too close a comparison of numbers until it has been possible to carry out extensive investigation of catches with the Recorder and catches of horizontal and vertical nets taken at the same places and times, to decide statistically how good a measure of the relative proportions of the constituent species is gained by horizontal hauls at one level (10 metres). An analysis made in 'Bulletin' No. 4 (p. 180) gives some confidence in the values obtained for the commoner species, but it is known that a differential depth preference exists for other species, e.g. *Anomalocera patersoni* for the upper few metres and *Euchaeta norvegica* and *Calanus hyperboreus* for deeper water.

However, taking a broad view, the forms caught fall into two distinct categories : those which are recorded in proportions which materially affect the total catch, and those which only occur in numbers low enough to be insignificant in relation to the whole. The former category, which includes *Calanus finmarchicus*, the Pseudocalanus group, *Temora longicornis,* Acartia spp. Centropages spp. and Oithona spp., so far outweighs the latter numerically that it can be said to include all the forms which from their food value in the sea have economic importance.[1]

The second category includes a larger number of species, which possibly because of their general scarcity, appear to have a more restricted distribution in space and time. These are in themselves interesting, and their distribution may provide useful clues in understanding the ecology of the area and the causes of the success or failure of the commoner forms. Some are certainly indigenous but nevertheless consistently less successful, while others may only occur in larger numbers outside the area, but are sufficiently tolerant to stand some mixture of their optimal environmental conditions and those conditions holding in the North Sea.

Four Types of Distribution.

Broad spatial differences in the population are immediately apparent. During the period under consideration there seems to be a boundary lying west to east from about the Firth of Forth to the coast of Denmark south of the entrance to the Skaggerak. South of this line, usually during the summer and latter half of the year, *Labidocera wollastoni, Parapontella brevicornis, Isias clavipes* and *Corycaeus*

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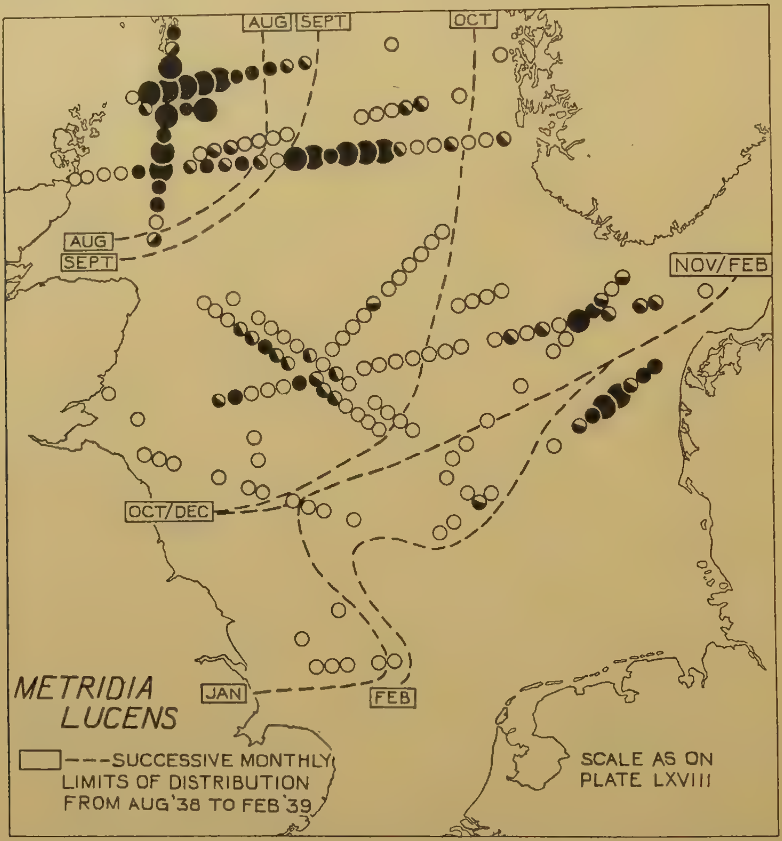
[1] Such a statement clearly begs the question of selective feeding, but the examples which make the case for the actual selection of copepods by the predator in this area refer to these common forms (Lebour, 1919 and 1921 ; Hardy, 1924 ; Ogilvie, 1938 ; and others). Instances have been reported of fish being packed with Labidocera, Anomalocera and Metridia in areas where these have occurred in dense swarms, but clearly the opportunity for such gorging rarely presents itself in the North Sea, and usually the predator, should it have any preference, must make its selection from the relatively abundant forms.

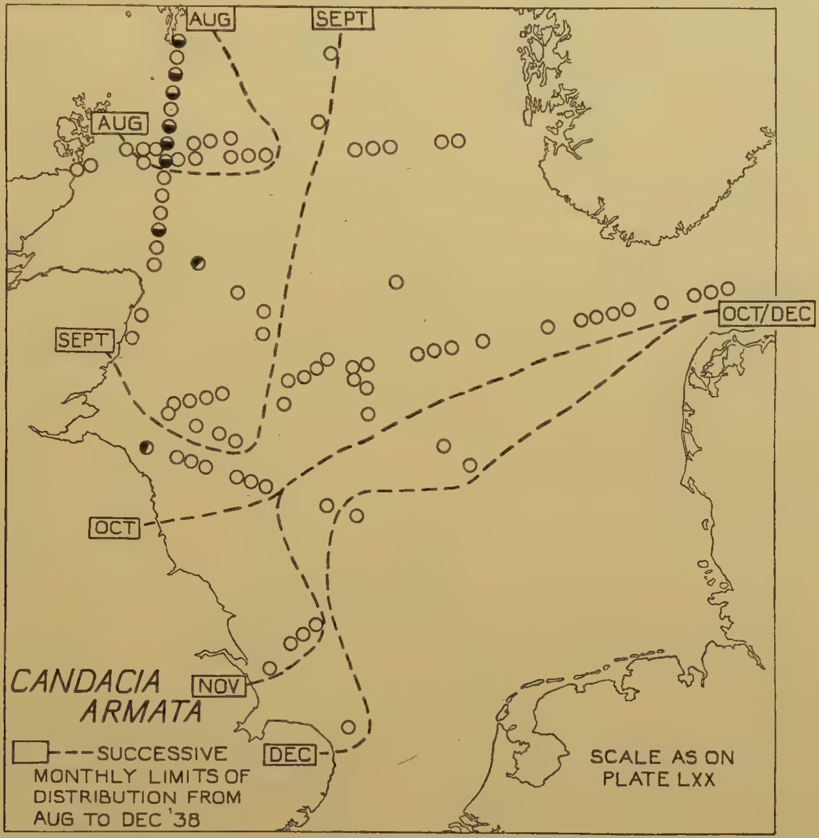
anglicus were taken, and extremely rarely were they found to the north of it. On the other hand, *Metridia lucens, Candacia armata, Calanus finmarchicus, Calanus hyperboreus, Euchaeta norvegica* and *Centropages typicus* were clearly more at home to the north of this line. The Pseudocalanus group, *T. longicornis* and Acartia spp., are not so easily defined. It is possible, however, to go a stage further and to differentiate between four distinct types of distribution. It is convenient first to define these four distributions by examples, and then return to consider their significance. To facilitate this, composite charts for six selected species have been prepared as Text-figs. 3–8. For each species the highest number recorded on each ten mile block throughout the 20 month period is represented by a symbol. It may be noted that on blocks where a species occurred on several occasions the numbers are not summed but the highest observation alone is taken.



Text-fig. 3.—A chart showing the overall distribution of *Metridia lucens* in the North Sea, from January, 1938, to August, 1939. The highest number taken on each " ten mile block " is represented by a symbol, the blacked-in symbols denoting the higher numbers in accordance with the scales on the monthly charts. The broken lines represent the *approximate* south-eastern limits of the distribution, month by month, from August, 1938, to February, 1939. For further explanation see p. 114 and footnote on p. 116, and for the monthly distribution charts see Plates LXVIII and LXIX.

The North-Western Forms.

Text-figs. 3 and 4 show a remarkably close agreement between the overall distribution of the two "oceanic" species, *M. lucens* and *C. armata.* The former was considerably more abundant, but nevertheless both show their maximum concentration in the Orkney–Shetland region. Although, possibly as a result of its relative abundance, the spread of *M. lucens* into the North Sea is slightly more marked, both species show the same *bulge* in their southernmost boundary to exclude the shallower waters over the Dogger Bank. A characteristic of their boundary is its movement into the North Sea during the late summer and autumn,

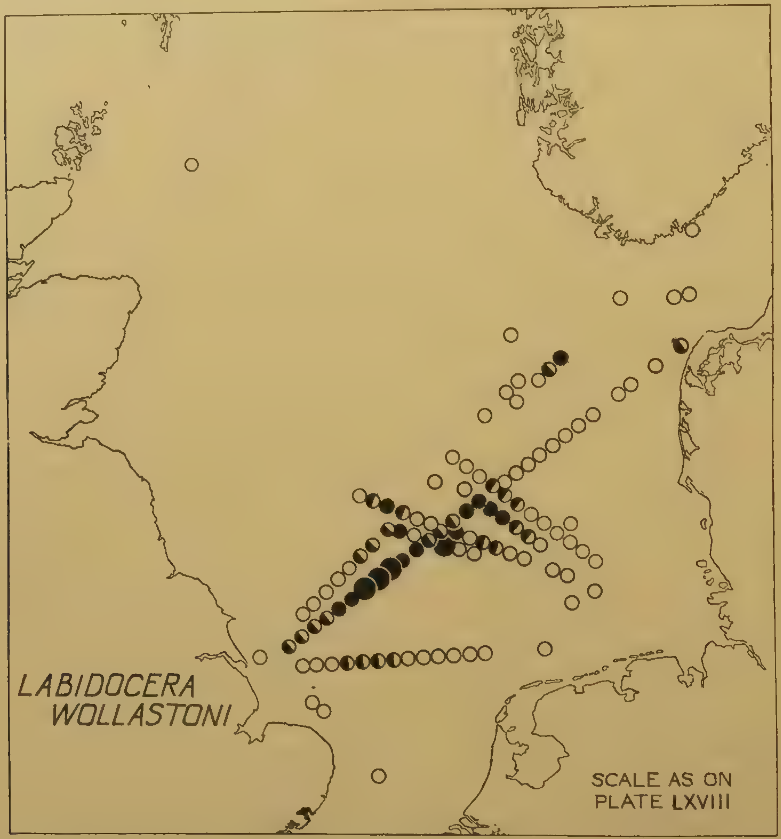

AUG
SEPT
AUG
SEPT
OCT/DEC
OCT
CANDACIA ARMATA
NOV
DEC
---SUCCESSIVE MONTHLY LIMITS OF DISTRIBUTION FROM AUG TO DEC '38
SCALE AS ON PLATE LXX

Text-fig. 4.—A chart showing the overall distribution of *Candacia armata* in the North Sea, from January, 1938, to August, 1939. The highest number taken on each "ten mile block" is represented by a symbol, the blacked-in symbols denoting the higher numbers in accordance with the scales on the monthly charts. The broken lines represent the *approximate* south-eastern limits of the distribution, month by month, from August to December, 1938. For further explanation see p. 114 and footnote on p. 116, and for the monthly distribution charts see Plates LXX and LXXI.

and contours are drawn in each case to show the approximate south-eastern limits of its penetration month by month.[1]

The North-Eastern Forms.

In Text-fig. 7 *C. hyperboreus* and *E. norvegica* are shown to be restricted to a broad band of water off the south and south-west coasts of Norway, including the mouth of the Skaggerak.



Text-fig. 5.—A chart showing the overall distribution of *Labidocera wollastoni* in the North Sea from January, 1938, to August, 1939. The highest number taken on each " ten mile block " is represented by a symbol, the blacked-in symbols denoting the higher numbers in accordance with the scales on the monthly charts. For further explanation see p. 114, and for the monthly distribution charts see Plates LXVIII and LXIX.

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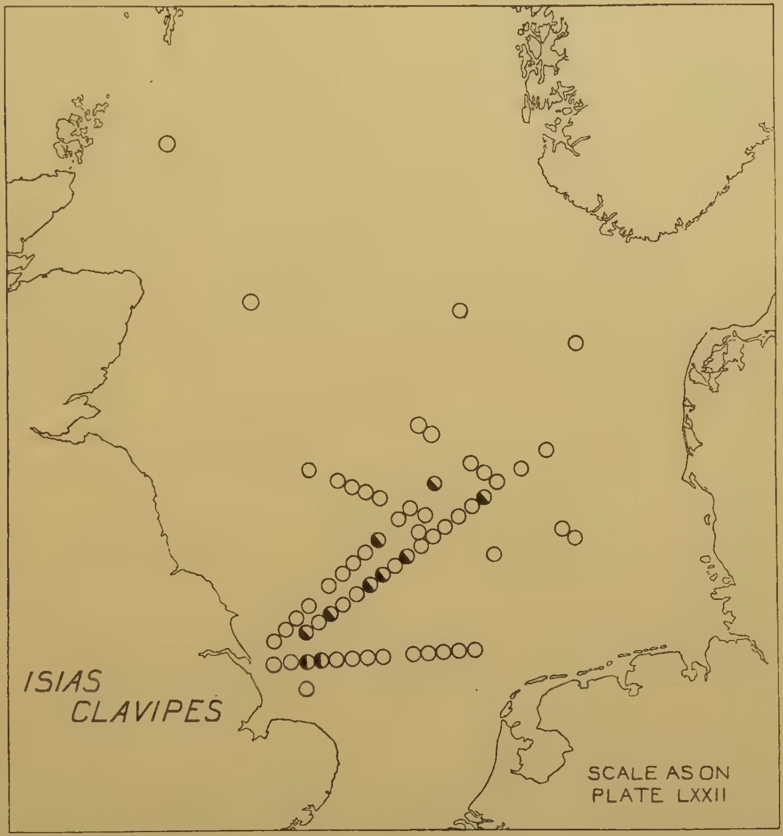
[1] It is important to realize that not all the occurrences to the north-west of any one of these boundary contours were necessarily recorded before or during the month for which the contour is drawn. For example in the case of *M. lucens*, it can be seen from Plate LXVIII, that the denser concentrations, which in Text-fig. 3 lie within the August contour, were actually recorded in September and October and did not reach further east until November; again the concentration to the south-east of the February contour were recorded in February, 1938. The contours are superimposed on the overall distribution for the 20 months, and denote the limits of the south-eastern penetration in the particular month.

The Central North Sea Forms.

There is also a very close agreement in space between *L. wollastoni* and *I. clavipes* (Text-figs. 5 and 6). The centre of concentration is over the south-western end of the Dogger Bank, and although they cover the central North Sea, they seem to be orientated along an axis stretching from the mouth of the Humber towards the Skaggerak.



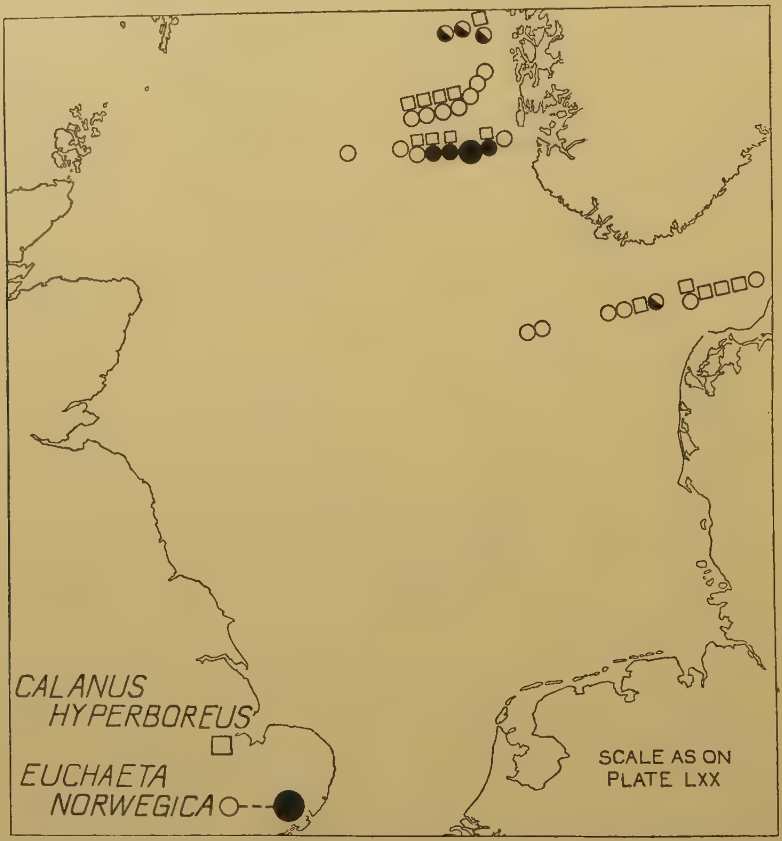
TEXT-FIG. 6.—A chart showing the overall distribution of *Isias clavipes* in the North Sea from January, 1938, to August, 1939. The highest number taken on each " ten mile block " is represented by a symbol, the blacked-in symbols denoting the higher numbers in accordance with the scales on the monthly charts. For further explanation see p. 114, and for the monthly distribution charts see Plates LXXI and LXXII.

A South-Eastern Form.

The overall distribution of the cyclopoid *C. anglicus* (Text-fig. 8) is complementary to that of the North-Western forms above. It is most abundant in the European coastal waters from Denmark to Holland, but nevertheless extends offshore well into the centre of the North Sea and approximately to the south-eastern limits of *M. lucens* and *C. armata*.

The Use of the Copepoda as Indicator Species.

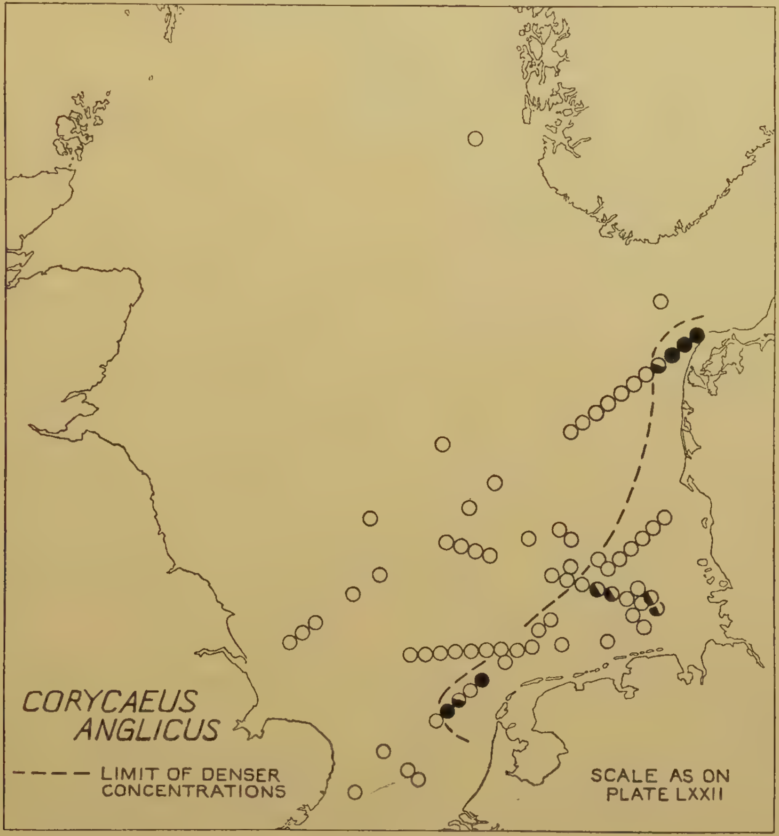
The question now arises as to whether these distributions are characteristic of different and identifiable water masses in the area. In fact, to what degree may we expect the type species used to prove useful indicators of water movement or the extent of outside influences in the North Sea?



Text-fig. 7.—A chart showing the overall distribution of *Calanus hyperboreus* and *Euchaeta norvegica* in the North Sea from January, 1938, to August, 1939. The highest number taken on each " ten mile block " is represented by a symbol, the blacked-in symbols denoting the higher numbers in accordance with the scales on the monthly charts. For further explanation see p. 114, and for the monthly distribution charts see Plates LXX and LXXI.

Russell (1939) has reviewed contemporary work on Indicator Species. By summarizing his own work, that of Fraser (1937, 1939) in the north, and that of Wulff (1934), Wulff, Bückmann and Künne (1934), and Künne (1937) in the south, he has differentiated between a number of types of water in and around the North

Sea, and has defined each in terms of the plankton it may be expected to carry. Many of the Indicator Species used are soft-bodied forms, which we have not so far been able to identify even if they have occurred in the Recorder catches. Of the more robust organisms, on the whole the Copepoda are seldom used as indicators. Nevertheless there are a number of other relevant forms which were identified in the Recorder material in 1938 and 1939, and which have been considered in 'Bulletins' Nos. 8 and 9 (Lucas, 1941, 1942) and 'Bulletin' No. 13 (Marshall, 1947).



TEXT-FIG. 8.—A chart showing the overall distribution of *Corycaeus anglicus* in the North Sea from January, 1938, to August, 1939. The highest number taken on each "ten mile block" is represented by a symbol, the blacked-in symbols denoting the higher numbers in accordance with the scales on the monthly charts. The broken line represents the approximate limit of the denser concentrations. For further explanation see p. 114, and for the monthly distribution charts see Plates LXXI and LXXII.

In the north, Fraser (1937, 1939) described "oceanic" water comprising a warm "Atlantic" element and a cold "Arctic" element which entered the North Sea past the Shetlands, and so became mixed with the Scottish coastal waters to give rise to what he termed "mixed oceanic and coastal water." If we consider only the plankton which has been identifiable in the Recorder material, this water, according to Fraser, was characterized by *Sagitta elegans*, Themisto (no specific identification given) and *Limacina retroversa*, together with an abundance of *C. finmarchicus*. Further south, in the region of the Dogger Bank, Künne (1937) identified what he termed " Northern Water," which he believed to be a mixture of oceanic and coastal water carried down from the north-west. This water, reasonably enough, contained some species common to the " mixed oceanic and coastal water " of Fraser, and in Künne's list of characteristic forms we find the following, which have been taken during the Recorder survey: *Sagitta elegans*, *Nyctiphanes couchii*, *Themisto abyssorum*, *Clione limacina* and *Limacina retroversa*. It is quite clear from the Recorder results that in 1938–1939, at least, the north-western copepods described above were associated with these types of water, and that *M. lucens* and *C. armata* were indicators of its movement. Marshall (1947) shows a close parallel between the distribution of these species of copepods and that of *C. limacina* and *L. retroversa*. They appeared together south of the Shetlands in the summer, and spread southwards in the main body of the North Sea during the succeeding months. *S. elegans* also showed from July, 1938, onwards a progressive extension of its habitat southwards culminating in the early months of 1939, and although it was present off the Shetlands throughout the period there is no doubt that it was more abundant there in the autumn when the other " northern indicator " forms appeared. Künne's other two indicator species, *N. couchii* and *Th. abyssorum*,[1] were alike in their behaviour, but did not conform to the expected distribution of " northern forms." It is true that they both appeared off the Shetlands in July or August of each year with the other " northern forms," and possibly spread from there into the North Sea, but they became so effectively established in the central and southern parts of our area that one might suspect some development of an indigenous stock. In fact, as we shall see later, their behaviour was more like that of *C. typicus*. Einarsson (1945), in his comprehensive review of the Euphausiacea in these waters, attacked most strongly the belief of Mielck (1925) and Künne (1937) that *N. couchii* was an indicator of the northern oceanic water entering the North Sea. He considered it to have " established itself as a permanent inhabitant of those English and Scottish coastal waters that adjoin the south-flowing oceanic current," and added, " With more right it could thus be claimed as an indicator of mixed coastal and oceanic water, penetrating into the southern North Sea, but it seems on the whole an unsuitable indicator as it is not confined to any distinct type of water in this area."

Other forms showed some *extension* southwards and eastwards from what appeared to be a very productive area off the Shetlands. Amongst these were *Thysanoessa inermis*, mostly young stages, (Marshall, 1947), and a number of phytoplanktonts (Lucas, 1941, 1942). Whether such extensions were indicative of water movement or local development will be discussed in a subsequent ' Bulletin,' but we may point out here that there were signs of two periods during which this extension of the zooplankton took place, one about May and the second about August or September, and they may well have been related to the spring and autumn phytoplankton crops.

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[1] *Th. gracilipes* (Norman) was not distinguished from *Th. abyssorum* (Boeck) in this material. (See Marshall's footnote to his section on *Th. abyssorum*).

L. wollastoni and *I. clavipes*, which we have considered typical of the "Central Distribution," are apparently indigenous to the central North Sea. There is no indication of effective recruitment of this population from the north or the south, and both species must fit into what Russell (1939) in his synopsis terms "the, so to speak, resident plankton population of the North Sea water," which is characterized by the general paucity of plankton and so far has *S. setosa* as its only indicator (Fraser, 1938). The contemporary Recorder data (Marshall, 1947) showed *S. setosa* to be well represented within the boundaries of these copepods but more widespread. In the first place, as we found when comparing *S. elegans* with the north-western copepods, it was present in appreciable numbers throughout the year. Secondly its northern limit was further north and its southern limit appeared to the south of our extreme observations. The same was true of the amphipod *Apherusa clevii*, which, although it had a distribution generally similar to the two copepod species in mid-summer when they were most abundant, had a more widespread and southerly distribution in the winter, when it in turn became more abundant.

If one considers the configuration of the floor of the North Sea, one is tempted to associate the distribution of *L. wollastoni* and *I. clavipes* with water depth. The northern limit of their distribution is, when compared with some other forms, relatively static, and follows approximately the line at which the sea shallows to the 30 fathom contour. They might conceivably be regarded as deeper water forms which have their vertical distribution upset by the increased upwelling and turbulence prevailing over the banks. However, as we have seen, the copepods which are undoubtedly carried towards the shallower water in the southward drift, *C. armata* and *M. lucens*, are singularly absent over the banks. Until further evidence has accumulated, we prefer to believe that these forms have their centre of concentration in the region of the Dogger Bank, and remain during the summer and autumn more or less contained within the Dogger Bank swirls.

L. wollastoni and *I. clavipes* have been associated in both space and time in each summer and autumn since the beginning of the Recorder survey in 1932 (Rae and Fraser, 1941), and it is interesting to note that in the autumn of 1933 when *I. clavipes* had a more southerly distribution and extended well south to the Hull to Rotterdam line, *L. wollastoni* was also well represented there.

Our south-eastern form, *C. anglicus*, from its distribution might be expected to be associated with Russell's "Flemish coast water, occurring along the Belgian and Dutch coasts," which "becomes mixed along its offshore boundary with channel water and moves in a north-easterly direction along the Jutland coast." Künne (1937) gave the pelagic hydroid, Clytia, for which we have no Recorder data, as being typical of this water. Wulff, Bückmann and Künne (1934), whose observations were restricted to the winter of 1933, mention Clytia and the larger numbers of copepods, suggesting *Temora longicornis* as typical but making no comment about *C. anglicus*. Further, they listed the following diatom and dinoflagellate species for which the Recorder findings for 1938 and 1939 have been published (Lucas, 1941, 1942): *Paralia sulcata*, *Bellarochea malleus*, *Guinardia flaccida*, *Thalassiothrix nitzschioides*, *Ceratium fusus* and *Ceratium furca*. Comparing the distribution of these species with that of *C. anglicus* in 1938 and 1939, we find that *P. sulcata* and *G. flaccida* were far more widespread, extending well over the area sampled. *Thx. nitzschioides*, although common in the central and northern North Sea, was singularly absent from this south-eastern area, while *B. malleus* showed a similar south-easterly restriction to that of *C. anglicus*. Both the dinoflagellate species formed a south-eastern population from June to September which was somewhat earlier than *C. anglicus*, but also had a well-marked and separate centre of concentration in the north-west of the area near the Shetlands where no *C. anglicus* was found. However, some of the diatoms illustrated by Lucas (1941) did show to a varying extent a south-eastern restriction similar to that of *C. anglicus*. *Biddulphia alternans* and *Bacteriastrum* spp. (probably *B. hyalinum*) occurred together in this region between August and October when *C. anglicus* was present and they appeared to be moving northwards along the Danish Coast, but the closest parallel was with *Biddulphia sinensis*. A comparison of the plates for the two forms in 'Bulletins' Nos. 3 and 4 shows that, although their years of relative success and failure did not coincide, there was nevertheless a striking agreement between their times of appearance each autumn and the positions of their concentrations. Wulff, Bückmann and Künne (1934) placed *B. sinensis* as an indicator of "pure channel water," but on the evidence now available we cannot have confidence in this as an unqualified statement. Ostenfeld (1908) concluded that it bloomed in a number of centres each year, and amongst his examples gave the Skaggerak and the waters off the mouth of the Elbe and the Dutch coast. This is in complete agreement with our findings that usually the first signs of the autumn flowering occurred near the Heligoland Bight, whilst patches on the Hull to Rotterdam line occurred later. This eastern area and the waters immediately to the south of the Dogger Bank have seemed to be the centres of maximum production, whereas the regions sampled by the Recorder which lie in the course of the high salinity current flowing through the Straits of Dover have always supported a weaker population.

Amongst the zooplankton, other than the Copepoda, identified in the Recorder material in 1938–39 (Marshall, 1947), the Echinoderm larvae, the Decapod larvae and the caprellid, *Phthisica acaudata*, showed a preference for the south-east of the area. The two former were not entirely absent from the north-west, and being composite groups are of little value as indicators. The caprellid is, however, more interesting in that it has been consistently present with *C. anglicus* and *B. sinensis* in each autumn since 1932 (*cf.* Henderson and Marshall, 1944). It tended to appear somewhat earlier in the year, in July or August, and seemed to have its main concentration further to the south, as it was almost invariably more abundant on the Hull to Rotterdam line than on the more northerly routes, and often appeared to spread northwards along the coast, whilst the usual spread of

B. sinensis started from the German end of the Bremen line. One would not expect a tychopelagic form, such as a caprellid, to be so much affected by lateral water movements as the more typical planktonic forms. In fact, a more obvious explanation of its appearance in a plankton community is the onset of increased turbulence or vertical mixing, which at the same time may stimulate the autumn flowering of *B. sinensis*. One might be tempted to attribute the tychopelagic habit to *C. anglicus* as well, in the southern North Sea at least, but although comparatively little has been written on the subject, we have Sars' (1918) statement that " It (*C. anglicus*) is . . . a pronouncedly pelagic animal, which has its true home in the open sea and only quite accidentally is thrown by the currents nearer to the shores and into the Fjords." Further, we know that it is quite commonly found in the western reaches of the channel, and a line of stations off Plymouth in 1933 showed it as an important member of the copepod population there in the late autumn and winter although absent during the spring and summer (Harvey, Cooper, Lebour and Russell, 1935). Yet, throughout our records, it has usually been scarcer on the Hull to Rotterdam line than immediately to the north and east, and there has been no satisfactory evidence of it having been recruited from the Channel during these years, although its distribution is doubtless influenced by variations in the Channel flow into the southern North Sea.

The fourth type of distribution found was that shown by *C. hyperboreus* and *E. norvegica*, which were essentially restricted to the north-eastern corner of the area under consideration above the deep water off the Norwegian coast. Throughout the 20 months *E. norvegica* was more often present than not, while *C. hyperboreus* only occurred from March to May, 1939. As we have already pointed out, workers are unanimous in the belief that both are deep and cold water species, and their restriction to deep water areas has been well demonstrated by Ruud (1929) and Sømme (1934), who showed them to be abundant in the deep fjords and offshore water but absent over the shallower coastal banks. Sømme, however, made it plain that at the time of its mass vertical migration (February–April) *C. hyperboreus* reached the upper layers, where it was subject to dispersal in any prevailing current. One might leave the consideration of their distribution with the observation that *C. hyperboreus* and *E. norvegica* occurred only in water more than 100 fathoms deep, and in the scope of our survey such water only existed off the Norwegian coast. But since this Norwegian area is so vital in the understanding of water movements in the North Sea, being the obvious exit and providing as it may the key to other movements in and out of the Skaggerak, we feel that further consideration is warranted.

There was a very close correlation in 1938 and 1939, both in space and time, between *E. norvegica* and *Meganyctiphanes norvegica* and some agreement with *Thysanoessa raschii* (*cf.* Marshall, 1947). Kramp (1913) described *M. norvegica* as a deep water form which might be carried into the North Sea through its north-western entrance with the colder elements of the Atlantic current but which was invariably present in the Skaggerak, where he believed offshoots of the stock in the

Norwegian Sea had established themselves.[1] *T. raschii* he found to be another northern species, also at home in the Skaggerak. Einarsson (1945), in his recent summary of earlier work, doubted the evidence for the Norwegian Sea origin of the Skaggerak population, but nevertheless agreed with the general picture of these distributions.

It seems that following the International Council's survey there was a general impression that the Skaggerak supported a rich, but isolated, community containing a number of species which were generally of more northern origin. We have mentioned Kramp's belief regarding *M. norvegica* ; Farran (1910) stated that the *M. lucens* stock in the Skaggerak was isolated, and his Plate XI for *C. hyperboreus* showed a concentration in the Skaggerak well removed from the otherwise northern habitat. Such an impression might have arisen from the very large number of stations occupied in the Skaggerak (their area 6), when compared with that part of the North Sea around the Norwegian coast and leading up to the Skaggerak (their area 7), but this is the less likely in that Kramp traced the continuity of the *Th. inermis* and *Th. raschii* population round the southern coast of Norway on one occasion, *i.e.* in the autumn of 1904, and many other zooplanktonts were shown as being generally plentiful in this region. The Recorder data for 1938 and 1939 gave some evidence of continuity of these forms through the allegedly barren coastal waters lying between the Norwegian Sea and the Skaggerak, because *C. hyperboreus*, *E. norvegica* and *M. norvegica* were often taken off Bergen, and at times as far round the south coast of Norway as our records extended. It is interesting to note that *E. norvegica* and *M. norvegica* were found together in May and August, 1939, over the deeper stretches of the Pentland Firth to Iceland records (' Bulletin ' No. 10, Lucas, Marshall and Rees, 1942), living in what we must assume to be mainly " Atlantic " conditions. Although from our evidence it is difficult to trace continuity of these species from there across the northern North Sea to the Norwegian coast or the mouth of the Skaggerak, such continuity is apparent, or at least may be inferred, for other north-western forms. Examples were *M. lucens* and *S. elegans* in the winter of 1938. It seems likely, as we have stated earlier, that certain north-western forms spread from the region of the Shetlands eastwards to the mouth of the Skaggerak, but we cannot entirely disregard what, at first sight, appears a less probable interpretation of the data, namely, that they spread westwards from the Skaggerak to join the north-western population. If one looks closely at the charts for *M. lucens* and *C. armata* for October, November and December, 1938 (Plates LXVIII and LXX), this appears to happen, but it must be remembered that our results are restricted to 10 metres, and movements in the deeper layers would not necessarily be apparent. Gran (1902) expressed the belief that *E. norvegica* entered the Norwegian coastal waters in the deeper elements of the Atlantic current, and it has been suggested the *S. elegans* may be carried to the mouth of the Skaggerak in deep currents while still absent in the upper layers.

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[1] It is interesting to note that although Kramp stated that the stocks found in the north-western part of the North Sea and in the Skaggerak were of different origin, he pointed out that in the Skaggerak *M. norvegica* was associated with the Arctic forms, *Diphyes arctica* and *Krohnia hamatus*, which Fraser (1937) found to be typical of the cold water element of the oceanic water entering the North Sea east of the Shetlands, and with *Aglantha digitalis*, which Künne (1937) used to identify water of north-western origin.

When considering the possible influence of the Skaggerak fauna on the copepod population in the North Sea, the behaviour of *C. typicus* is interesting in view of Scott's (1911) results. He, in his Plate XVII, showed it generally " rare " in the central North Sea but " common " or " abundant " during the summer and autumn quarters in the north-west, in the Skaggerak and in the western English Channel, and from the two former centres there was some extension into the body of the North Sea. In the earlier years of the Recorder survey this species was quite prominent in the southern Bight in the autumn. In 1938, as we have seen above, it was well represented off the Shetlands in late summer, and appeared to spread south and east at about the same time as *M. lucens*, *C. armata* and the other northern indicators, although the speed with which it became established in the central area in August clearly could not result from water movement alone. It is more likely that there was a contemporary increase in the population off the mouth of the Skaggerak.[1] In 1939 there were no signs of recruitment from the north-west, and the entire development of the species seemed to originate from the off Skaggerak area. While it has been conventional to look for populations which are carried into the North Sea from the north and through the Straits of Dover, one must not lose sight of the possibility of an invasion from the Skaggerak, where the water undoubtedly contains a rich fauna. Attention will be paid to this point as our information becomes more plentiful.

As stated above, the other, and in the main, commoner forms of copepods (*e.g.* Pseudocalanus, Temora and Acartia) were less conservative in their distribution and behaviour. It has been suggested that the apparent wider distribution might be in fact the result of their greater abundance. For example, had the Recorder aperture been cut down in cross-section still further, the now less common forms would have almost disappeared and the commoner forms would have appeared more restricted. To an extent, of course, this is true, but by successively charting the distribution of only those numbers exceeding x and then $2x$ and $4x$, etc., we have failed to find any restriction in their distribution which we can believe to have the significance that we have attributed to the four characteristic distributions described above.

However, even if their behaviour in space and time is too complex or inconsistent to warrant discussion until our observations have extended over a longer period, there are certain points to be borne in mind. Except for the north-eastern deep water forms, whose case is peculiar, all the species whose distribution we have defined above are late summer or autumn forms. On the other hand, these others, the commoner forms, reach their maxima earlier, and are mainly responsible for the enormous increase in the plankton in the spring. Earlier in this report (p. 102) we specified four areas in which this increase commenced : off the mouth of the Skaggerak, the north-eastern Scottish coast, the extreme south, and over the Dogger

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[1] The behaviour of *N. couchii* and *Th. abyssorum* is somewhat similar. (See p. 120.)

Bank. In the two more southerly areas of development, over the Dogger Bank and in the extreme south,[1] the Pseudocalanus group, *Temora longicornis*, Acartia spp. and *Centropages hamatus*, which we can consider to be the four commonest spring forms, all played their part in both 1938 and 1939. There was little noticeable difference in the extent of the copepod production in the two years, except in the extreme south, and, as has been pointed out by Lucas (1941 and 1942), the spring diatom and dinoflagellate crop was far less pronounced in the south in 1939 than 1938.

In the north and east, off the Scottish coast (and Shetlands) and off the mouth of the Skaggerak there were marked differences between the two springs. Off the Skaggerak in April, 1938, the increasing population was comprised almost entirely of *Calanus finmarchicus*, young and adult, with the commoner spring forms of copepods very poorly represented, whereas the following year there was a very strong development, including the *Pseudocalanus group*, *T. longicornis*, *C. hamatus*, and particularly large numbers of Acartia spp. In the north-west the situation was reversed, 1938 being by far the more successful year ; Pseudocalanus and Acartia were more abundant, and Temora, although not playing a major part until July in each year, was also more numerous. *Centropages hamatus* had similar values in each year.

This change between the spring of 1938 and the spring of 1939 in the region of maximum production of the commoner forms from west to east is one of the most striking points from the copepod data, more particularly so because the two regions concerned are so dissimilar hydrographically. In the north-west, at this time of year, we may expect relatively high salinities resulting from the admixture of " Atlantic water," which according to Tait (1937) has its greatest influence there in early spring. Off the Skaggerak, however, low surface salinities may be expected, as at about this time the Baltic effluent usually begins to make itself felt in the North Sea (Lucas and Rae, 1946, Text-figs. 2, 3). It is possible that this change appeared more pronounced in the Recorder data than it really was in fact, because, as can be seen, the off Skaggerak region was more adequately sampled in the spring of 1939 than 1938. Taking the broader view, however, it is plain that throughout the spring and summer season there was a more westerly distribution in 1938 and a more easterly one in 1939. The spring of 1939, in fact, seems to be characterized by activity in the north-eastern quarter. Lucas (1942) commented on the success of the spring dinoflagellate population there in 1939 when compared with the previous year. It was in early 1939 that *C. hyperboreus* appeared off the Norwegian coast and in the entrance to the Skaggerak, and in April, 1939, that *E. norvegica* was most abundant. Again, we have tentatively suggested that in 1939 the *C. typicus* population appeared to establish itself in the North Sea from the Skaggerak region with little or no assistance from the north-west. Such a change may well be associated with some pronounced difference in the hydrographical conditions prevailing. This will be considered further, when more information regarding salinities and temperatures are available.

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[1] The degree of development in the density of the population in the extreme south is small when compared with the other centres defined, but we prefer to include it, as it may well prove to have a significance in relation to the influence of the English Channel inflow in the southern North Sea.

General Remarks.

It may be felt that we have attempted to read more significance in the 1938–1939 copepod distributions than the 20 months' data warrant. Under normal circumstances we would have expected results from at least three completed years over the extended area to be required before this information was sufficiently secure for presentation. However, a break for the war years and an inevitable period for reorganization of the programme was unavoidable, and it seemed wiser to draft a schematic plan for the copepod distribution as early as possible, even if it would not be for some considerable time that we would be in a position to confirm it or modify it. There are certain points about this distribution as shown in the relatively small Recorder catches which have been impressively consistent since 1932, and which are not generally known. For example, there is the restriction of *C. anglicus* to the south-east in the autumn and winter, the agreement in the time and place of occurrence of *L. wollastoni* and *I. clavipes*, the arrival of *C. armata* and *M. lucens* as far south as the Humber in the autumn and winter of most years. These and other points convince us that there is a recognizable "characteristic" distribution of the copepod species in space and time, and it is reasonable to suppose that variations from this "normal distribution" will assist us to understand the ecology of the area. In many respects the variations are in themselves more interesting than the normal, and so we have stated our impression of the latter, using information taken over a short period and backed to a large extent by circumstantial evidence. Now that data are again forthcoming we hope to be able to confirm or deny these tentative conclusions.

We believe there is here promising evidence that the Copepoda fit into the general pattern of indicator species, and so may prove to be of more use in the understanding of water movements than previously expected. But in conclusion it may be as well to mention again some of the dangers involved in the interpretation of the movement of water masses in terms of plankton distribution. The limitations of such a process have been raised by a number of workers, and have been conveniently summarized by Russell (1936). Gran (1902) took a particularly practical view of the over-optimistic claims of earlier workers, but some of his objections become less serious when considering the data collected by a machine like the Continuous Plankton Recorder. In the earlier days one identified the plankton taken from a particular body of water, and, from previous knowledge of the distribution and habits of the constituents, surmised its past history by assessing the relative proportions of "oceanic," "neritic," "arctic," etc., species. With the Recorder, however, it is often possible to approach the problem in a different way. Sufficient information can be made available at short intervals of time to allow one to trace the actual movements of the boundaries of the distribution of communities or selected indicator species and so acquire positive knowledge of their origin. One can follow the stages in the process, rather than deducing the stages from the final result. Such positive data are satisfactory, but, as explained by Farran (1933), the danger lies in the interpretation of the negative data. For example, while the movement of a number of forms of known "oceanic" origin into the southern North Sea at any time may be considered fairly an indication of an admixture of oceanic water there, the failure of recognizably oceanic forms to enter at some later date does not necessarily postulate that this oceanic influence is absent or less pronounced, unless we can be confident that the indicators used are always present in comparable numbers at the source of the oceanic water. As we have seen above, in 1938 from July and August onwards there was a migration of a number of northern forms towards the south. These included *Metridia lucens*, *Candacia armata*, *Clione limacina* and *Limacina retroversa*. On this evidence we might conclude that this period was one of maximum north to south movement of water in the area. However, there was also evidence of *M. lucens* moving southwards to a lesser extent in May of both 1938 and 1939 without the other four species, and the fact that there was then a spread of the plankton to the south and east was confirmed by the behaviour of *Thysanoessa inermis* from May to July in each year and the general distribution of the north-western crop of diatoms and dinoflagellates in the spring. Clearly then, our ideas of water movement may be seriously biased by the seasonal distribution of the indicator species, *i.e.* their presence or absence in the water we wish to identify at any one time. We have seen *Labidocera wollastoni* and *Isias clavipes* in 1938 and 1939 pass through a seasonal cycle and a half in the central North Sea with their boundary in each direction delimited within the scope of our observations ; they were, in fact, an entire and self-contained population. And yet they were only present in catchable numbers, or available as indicators, for 10 of the 20 months at the most. It is reasonable to suppose that the seasonal fluctuations of other species are comparable.

Again, even if one restricts one's comparison of water movement from year to year to the season at which one has learnt from experience to expect a particular indicator species or group of species, there is still the danger of mistaking an unsuccessful year for the species in its own and more normal type of water for a year in which the movement of such water into the area of observation did not occur. Only a small fraction of the population can be expected to travel as exotics, and if the total population is at a low ebb, this fraction may be too small to be recorded in the invaded area. For example, in the autumn of 1938 *Centropages typicus* appeared to spread into the North Sea from the Shetland area with certain oceanic forms (p. 106). In 1939, although the other forms reappeared, *C. typicus* was absent, but we find also that it was poorly represented in the oceanic water sampled between April and August by the Iceland line (Lucas, Marshall and Rees, 1942). In fact, no matter how pronounced the flow of Atlantic water through the Faroe-Shetland Channel had been, it could not have been indicated by *C. typicus* in that year because it was so poorly represented.

The suggestion is, then, that conclusions regarding relative water transport based on plankton indicators may prove misleading unless one has good and contemporary knowledge of the composition of the plankton in the water mass at its source, and unless from experience one can say with confidence that there exists in the plankton typical of the water to be identified, indicator species which, when their seasons of abundance are added together, give a good coverage of the whole year. It is in fact essential that we obtain a better idea of the biology of our indicators, and with this in view we intend to select a number of possible indicators from amongst the copepods and attempt to work out their breeding cycles during the future Recorder survey. Such an investigation will not be comprehensive or detailed ; we realize with the material available it cannot be. But the degree of detail now being found by Mr. Rees for *Calanus finmarchicus* will allow us to meet the requirement of Damas and Koefoed (1907) contained in their most salient remark : " . . . the use of pelagic organisms as indicators is a local science, based on the knowledge of the special habits of each form, in the region considered."

SUMMARY.

1. The distributions of the various species of Copepoda taken by the Continuous Plankton Recorder along ten steamship routes in the North Sea from January, 1938, until August, 1939, are illustrated (Plates LXIII–LXXXVIII), described in turn, and compared with previous ideas regarding their habitats (pp. 101 to 112).

2. The population as a whole was found to increase rapidly from several centres in April or May, and to decrease during the summer and autumn to a generally low level in the winter. The sparse winter population was concentrated in the Heligoland Bight (pp. 101 to 102).

3. A few species were found to be responsible for the dense spring population. They were a *Pseudocalanus* group (comprising mainly *Pseudocalanus elongatus*, but including *Paracalanus parvus* and *Microcalanus pusillus*), Acartia spp., *Temora longicornis*, and in the north *Calanus finmarchicus* (pp. 125 to 126).

4. For the less abundant species four distinct types of distribution are defined. The first was that shown by the characteristically " oceanic " forms, *Metridia lucens* and *Candacia armata*, which are carried into our area from the Shetland area with the " mixed oceanic and coastal water." The second was a restriction to the coast of Norway and the mouth of the Skaggerak, as shown by the deep water forms, *Calanus hyperboreus* and *Euchaeta norvegica*. The third was a central North Sea distribution about the Dogger Bank shown by *Labidocera wollastoni* and *Isias clavipes*. Finally, there was a restriction to the south-east along the continental coast; *Corycaeus anglicus* was typical of this distribution (pp. 113 to 118).

5. These four distributions, discussed in relation to previous knowledge, are compared with the contemporary Recorder data for phytoplankton and other zooplankton forms (pp. 118 to 125).

6. The probable value of the Copepoda as indicators of water movement is discussed (pp. 127 to 129).

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EXPLANATION OF PLATES LXIII TO LXXXVIII.

PLATES LXIII–LXV.

A series of histograms showing the average monthly catch per mile on the Recorder lines in each of the sub-areas A–L of the North Sea (see key map on Plate and Text-fig. 2) for the Total Copepoda and some of the constituent forms. Information is given for each month from January, 1938, to August, 1939, except for Oithona spp., for which there were no data before September, 1938. Months in which the average was too low to be shown as a histogram are marked + ; months in which there were insufficient observations to warrant an average are marked *. The figures below each sub-area reference letter give the mean value of the catch per mile in that sub-area ; similarly for the whole area histogram.

PLATES LXVI–LXXXVIII.

Charts showing the distribution of the Total Copepoda and the various species of copepoda taken on the Recorder lines in the North Sea from January, 1938, to August, 1939. The symbols and/or numerals denote the varying quantities caught on each " ten mile block " as indicated by the appropriate scales. When more than one Record was taken on a route in any one month they are shown " in parallel " (the earlier one to the left or above). Details of the date and time of each Record are given in ' Bulletin ' No. 7.

PLATES LXVI AND LXVII.

Charts showing the distribution of the Total Copepoda, month by month, from January, 1938, to August, 1939.

PLATES LXVIII AND LXIX.

Charts showing the distribution of *Metridia lucens* and *Labidocera wollastoni*, month by month, from January, 1938, to August, 1939.

PLATES LXX AND LXXI.

Charts showing the distribution of *Candacia armata*, *Euchaeta norvegica* and some rarer species of Copepoda (indicated by letters), month by month, from January, 1938, to August, 1939. The inset shows the only catches of *Isias clavipes* and *Corycaeus anglicus* from January to August, 1939, and is a continuation of Plate LXXII (see below).

PLATE LXXII.

Charts showing the distribution of *Isias clavipes* and *Corycaeus anglicus*, month by month, from January to December, 1938. Charts for January to August, 1939, are included on Plate LXXI above.

PLATE LXXIII.

Charts showing the distribution of Acartia spp., month by month, from April to September, 1938. Catches exceeding 100 individuals per mile are underlined. The data for the remainder of the survey are shown on Plates LXXXIV and LXXXVII.

PLATES LXXIV AND LXXV.

Charts showing the distribution of *Calanus finmarchicus*, copepodite stages I–IV combined, month by month, from April to September, 1938, and April to August, 1939. Catches exceeding 50 individuals per mile are underlined. The data for the remainder of the survey are shown on Plate LXXXV.

PLATES LXXVI AND LXXVII.

Charts showing the distribution of *Calanus finmarchicus*, stages V and VI combined, month by month, from April to September, 1938, and April to August, 1939. Catches exceeding 100 individuals per ten miles are underlined. The data for the remainder of the survey are shown on Plate LXXXV.

PLATES LXXVIII AND LXXIX.

Charts showing the distribution of the Pseudocalanus group (comprising *Pseudocalanus elongatus*, *Paracalanus parvus* and *Microcalanus pusillus*), month by month, from April to September, 1938, and April to August, 1939. Catches exceeding 150 individuals per mile are underlined. The data for the remainder of the survey are shown on Plate LXXXVI.

PLATES LXXX AND LXXXI.

Charts showing the distribution of *Temora longicornis*, month by month, from April to September, 1938, and April to August, 1939. Catches exceeding 70 individuals per mile are underlined. The data for the remainder of the survey are shown on Plate LXXXVI.

PLATES LXXXII AND LXXXIII.

Charts showing the distribution of *Centropages typicus* (squares) and *Centropages hamatus* (circles), month by month, from April to September, 1938, and April to August, 1939. The data for the remainder of the survey are shown on Plate LXXXVII.

PLATE LXXXIV.

Charts showing the distribution of Acartia spp., month by month, from April to August, 1939. Catches exceeding 100 individuals per mile are underlined. (See also Plate LXXIII above.)

PLATE LXXXV.

Charts showing the distribution of *Calanus finmarchicus* in the months not illustrated on Plates LXXIV–LXXVII above.

PLATE LXXXVI.

Charts showing the distribution of the Pseudocalanus group in the months not illustrated on Plates LXXVIII and LXXXI above.

PLATE LXXXVII.

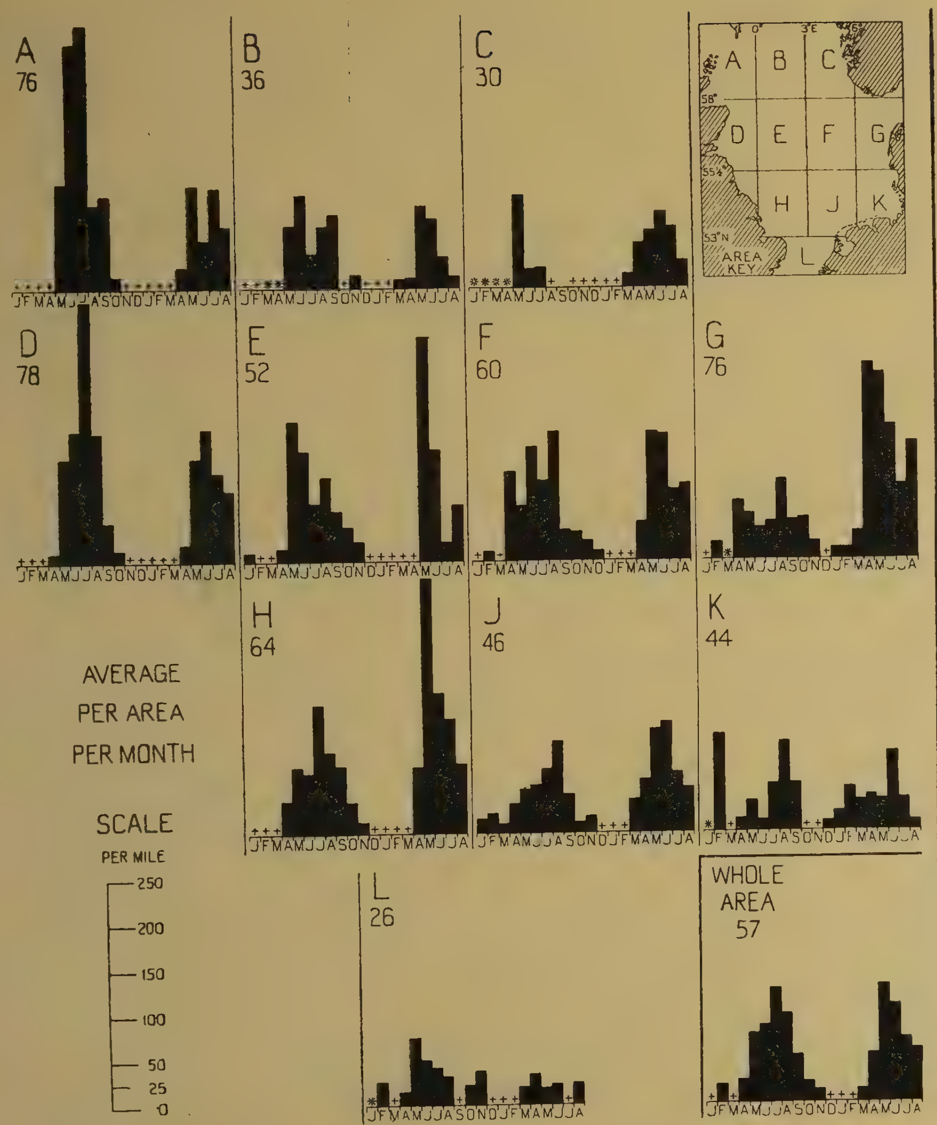
Charts showing the distribution of Centropages spp. and Acartia spp. in the months not illustrated on Plates LXXIII and LXXXII–LXXXIV above.

PLATE LXXXVIII.

Charts showing the distribution of Oithona spp. month by month, from September, 1938, to August, 1939. Catches exceeding 40 per mile are underlined. No data were available prior to September, 1938.

PLATE LXIII

TOTAL COPEPODA



OITHONA SPP.

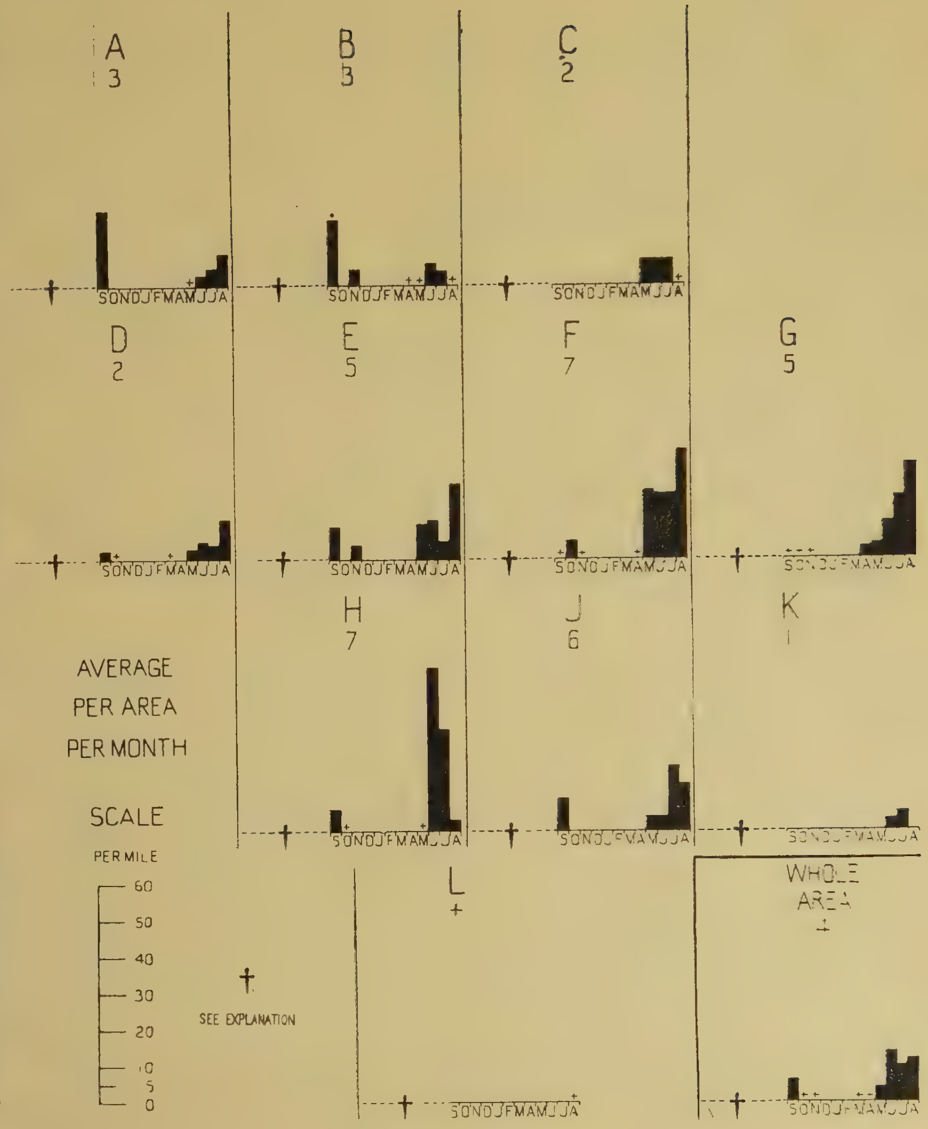
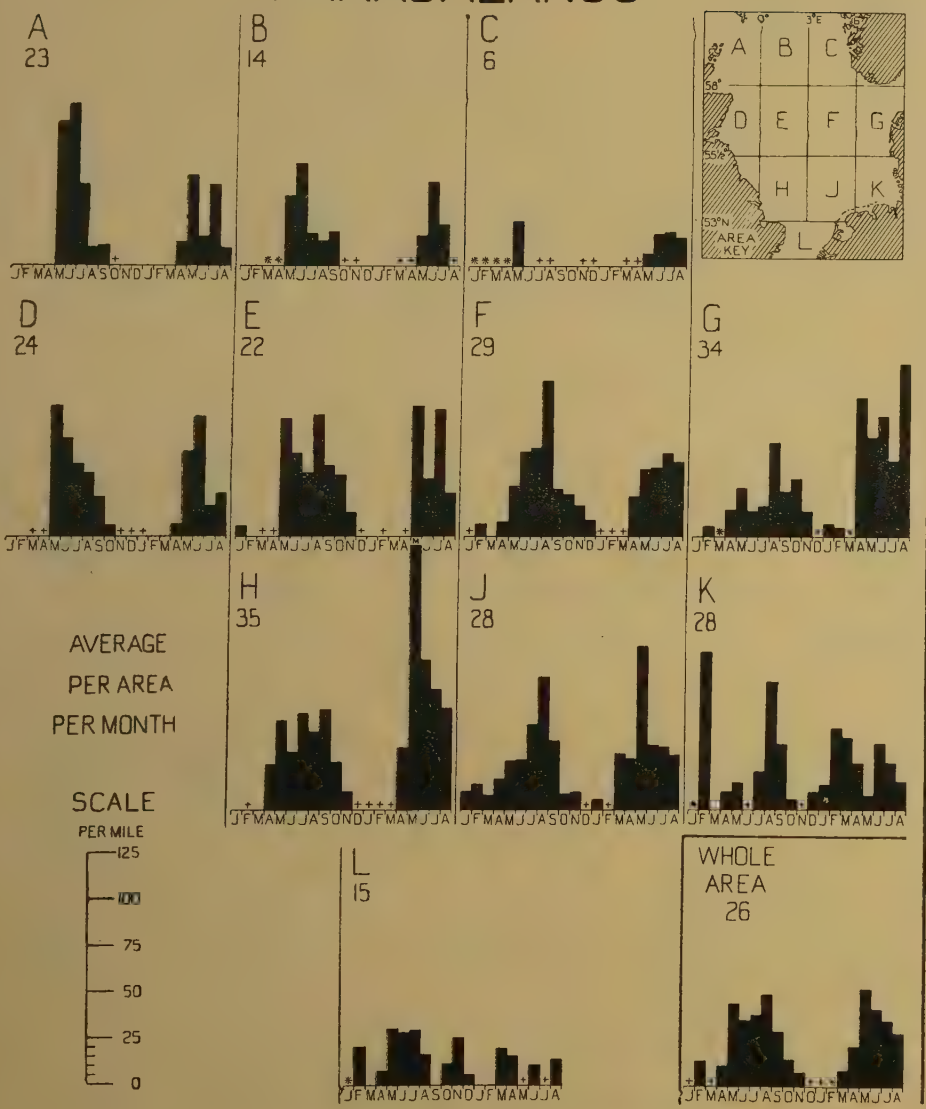


PLATE LXIV

PSEUDOCALANUS
+ PARACALANUS



TEMORA

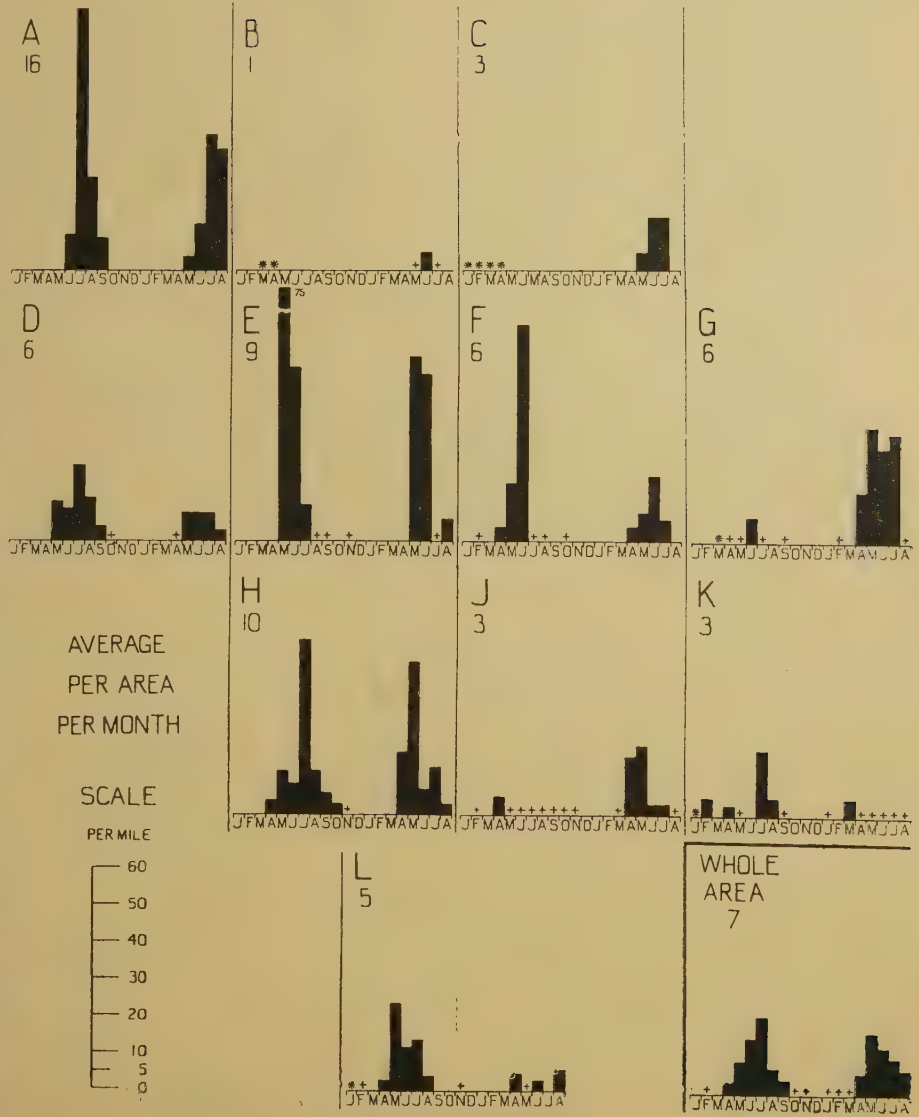
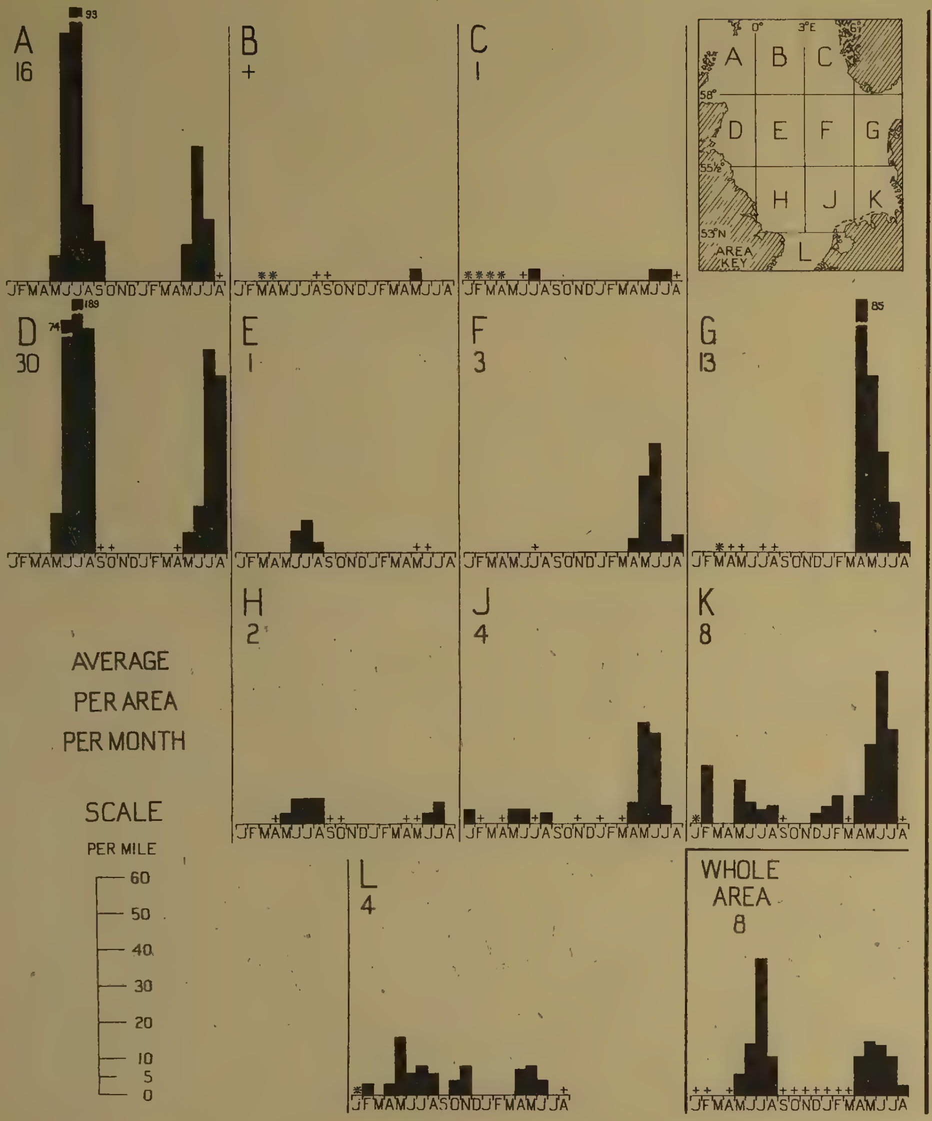
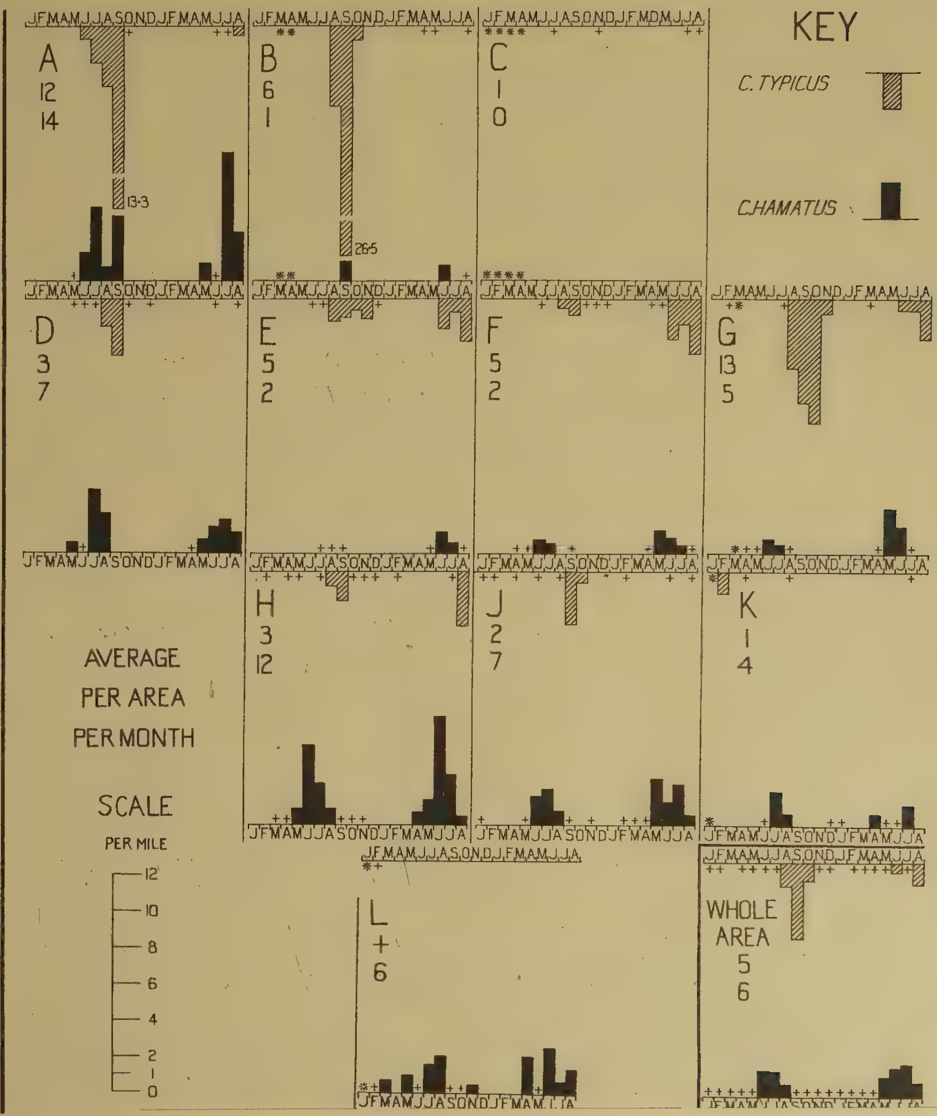


PLATE LXV

ACARTIA SPP.



CENTROPAGES SPP.



ERRATA, PLATE LXV: For Centropages spp., the figures below each sub-area reference letter, giving the mean value of the catches per mile for the whole twenty month period, should be divided by 10: e.g., A, 1·2 and 1·4; B, 0·6 and 0·1; whole area, 0·5 and 0·6.

PLATE LXVI

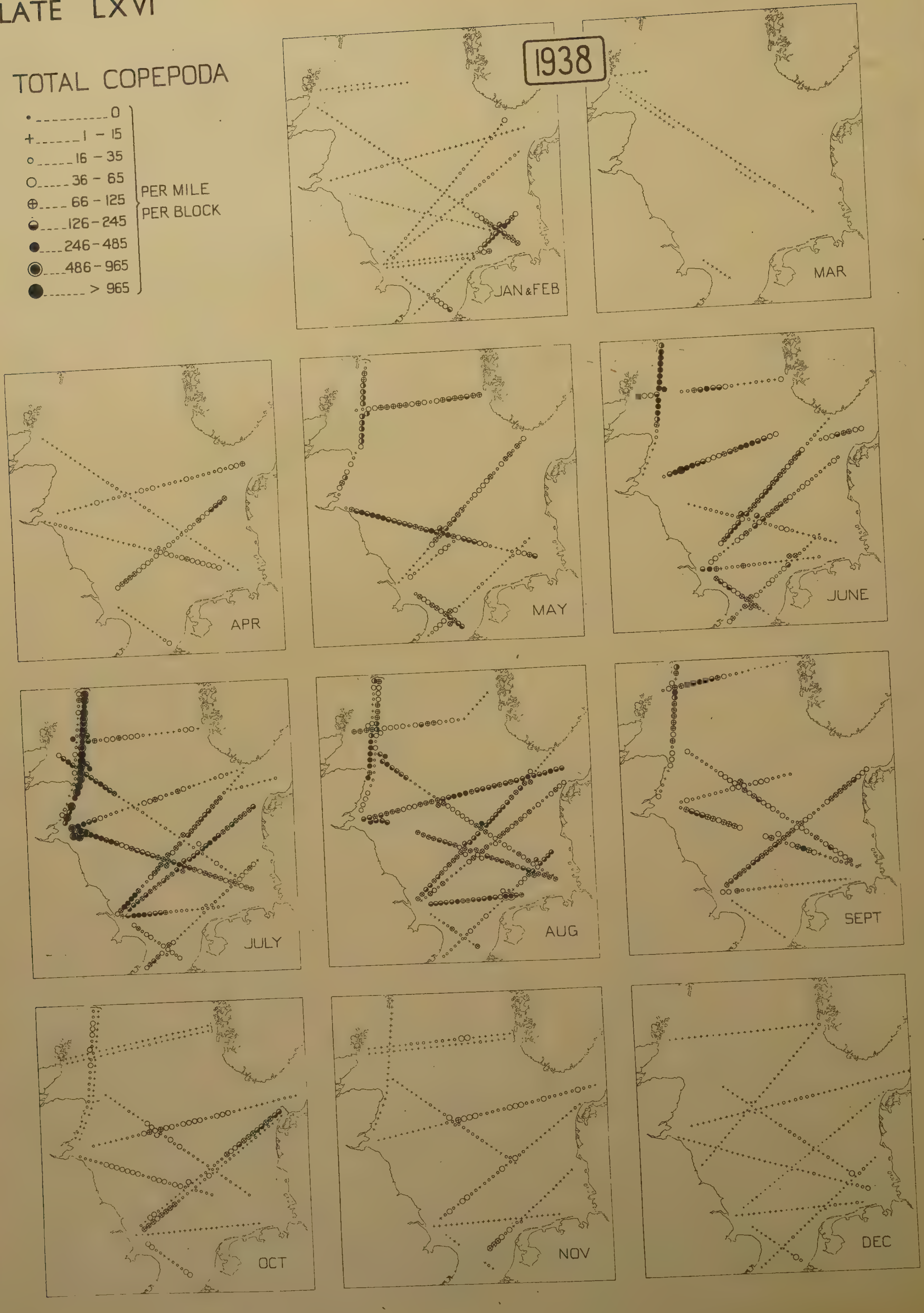

TOTAL COPEPODA
• 0
+ 1 – 15
∘ 16 – 35
○ 36 – 65
⊕ 66 – 125
◒ 126 – 245
● 246 – 485
◉ 486 – 965
● > 965
PER MILE PER BLOCK
1938
JAN & FEB
MAR
APR
MAY
JUNE
JULY
AUG
SEPT
OCT
NOV
DEC

PLATE LXVII

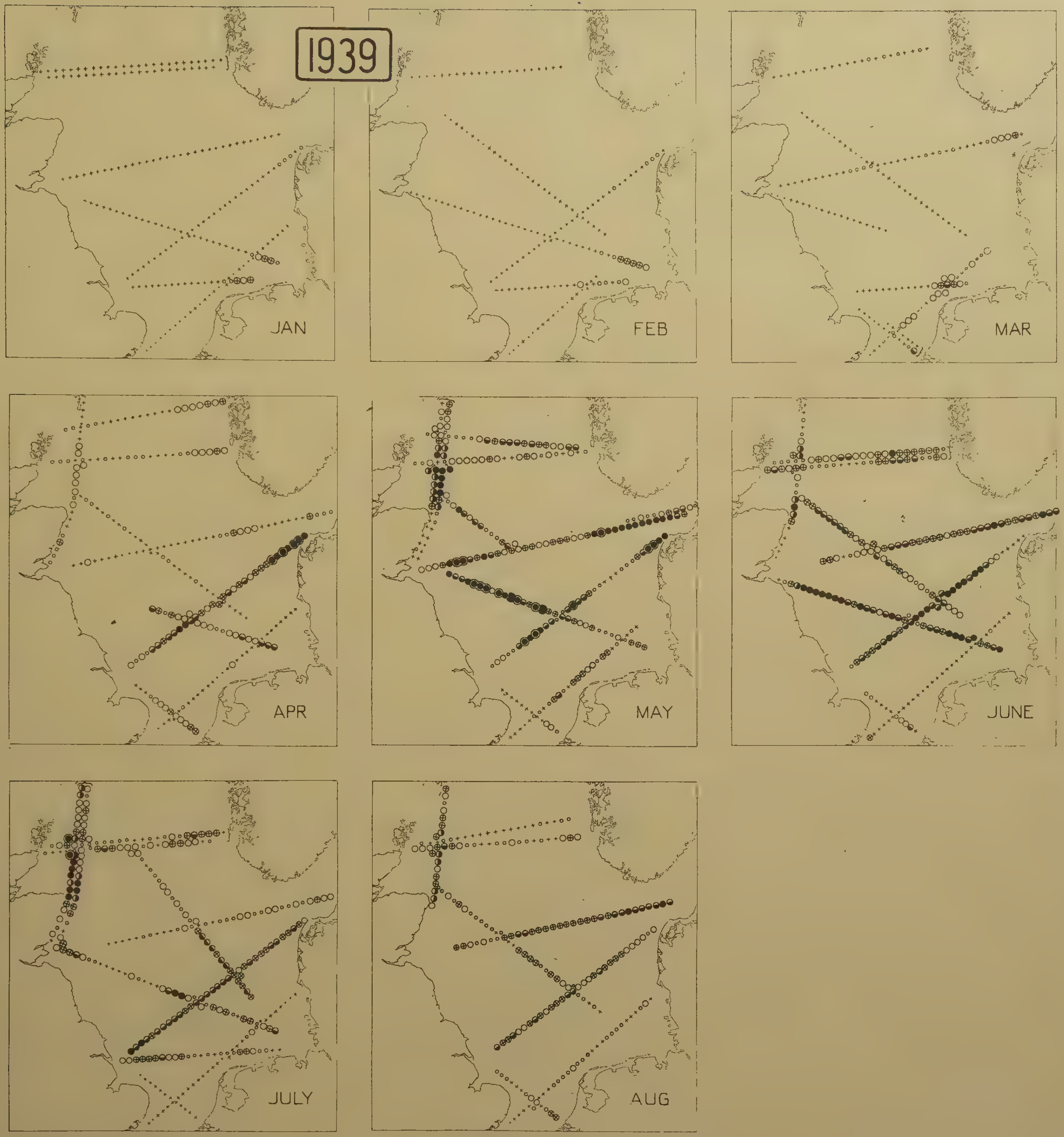

1939
JAN
FEB
MAR
APR
MAY
JUNE
JULY
AUG

PLATE LXVIII

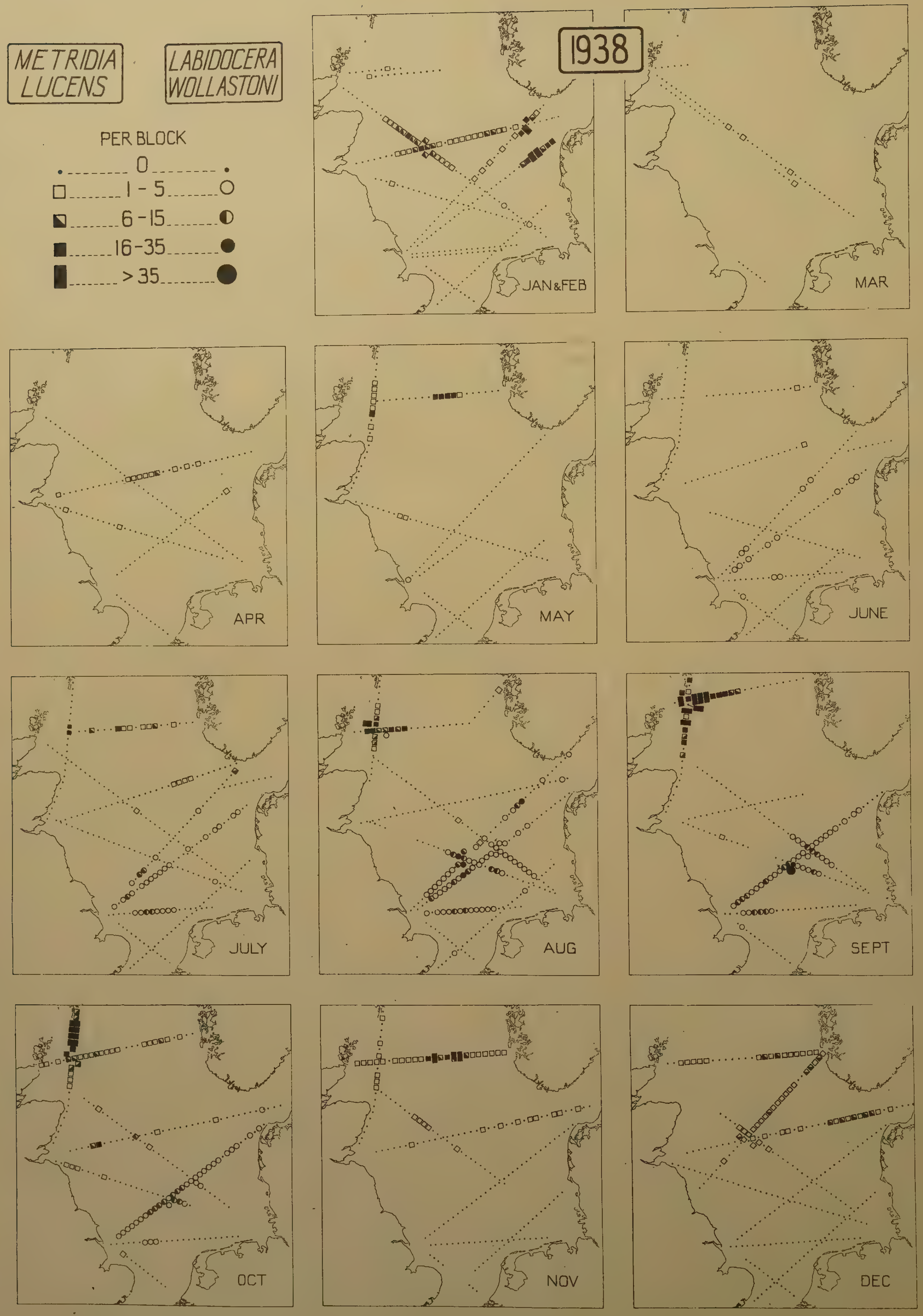

METRIDIA LUCENS
LABIDOCERA WOLLASTONI
PER BLOCK
0
1 - 5
6 - 15
16 - 35
> 35
1938
JAN & FEB
MAR
APR
MAY
JUNE
JULY
AUG
SEPT
OCT
NOV
DEC

PLATE LXIX

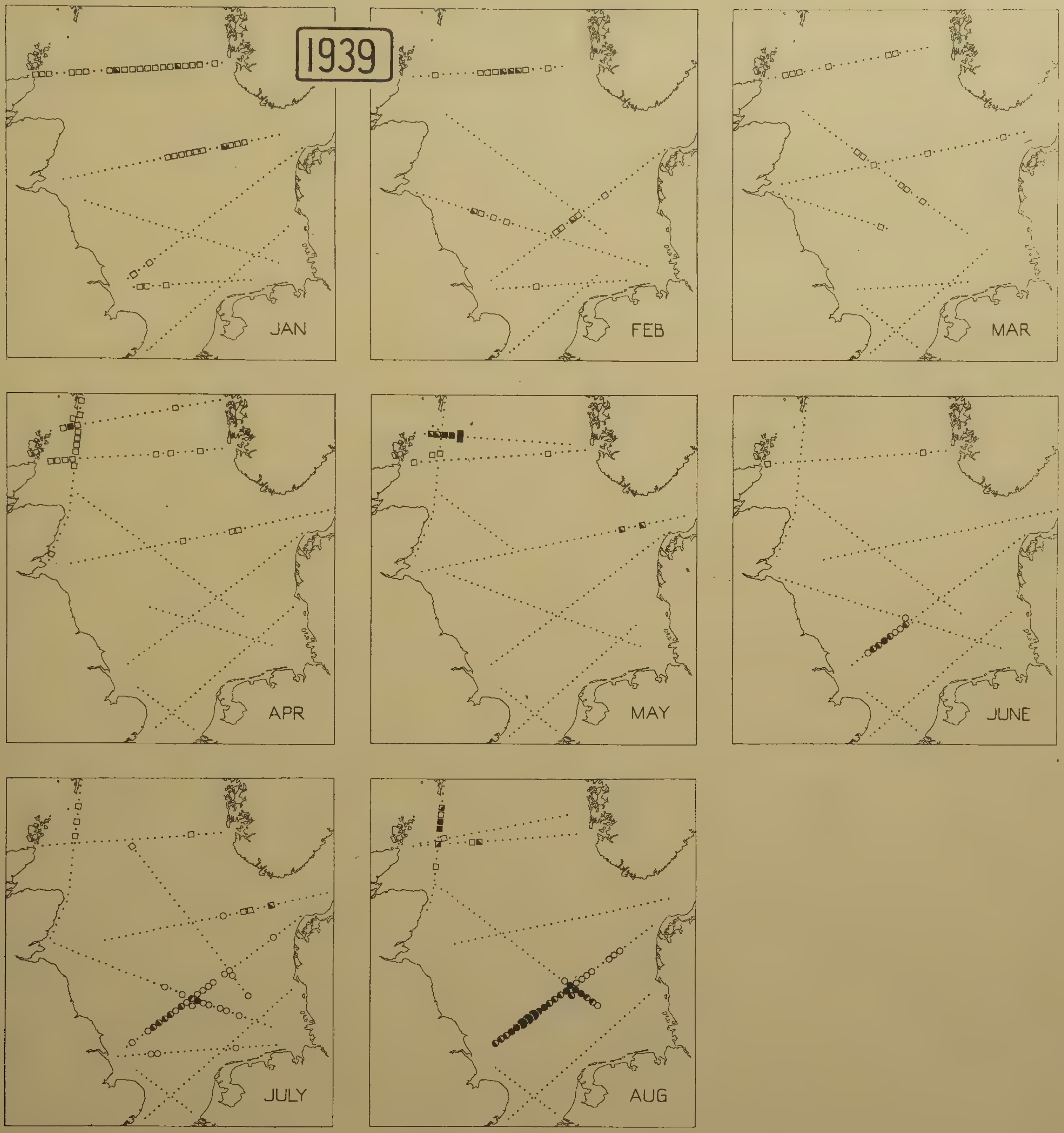
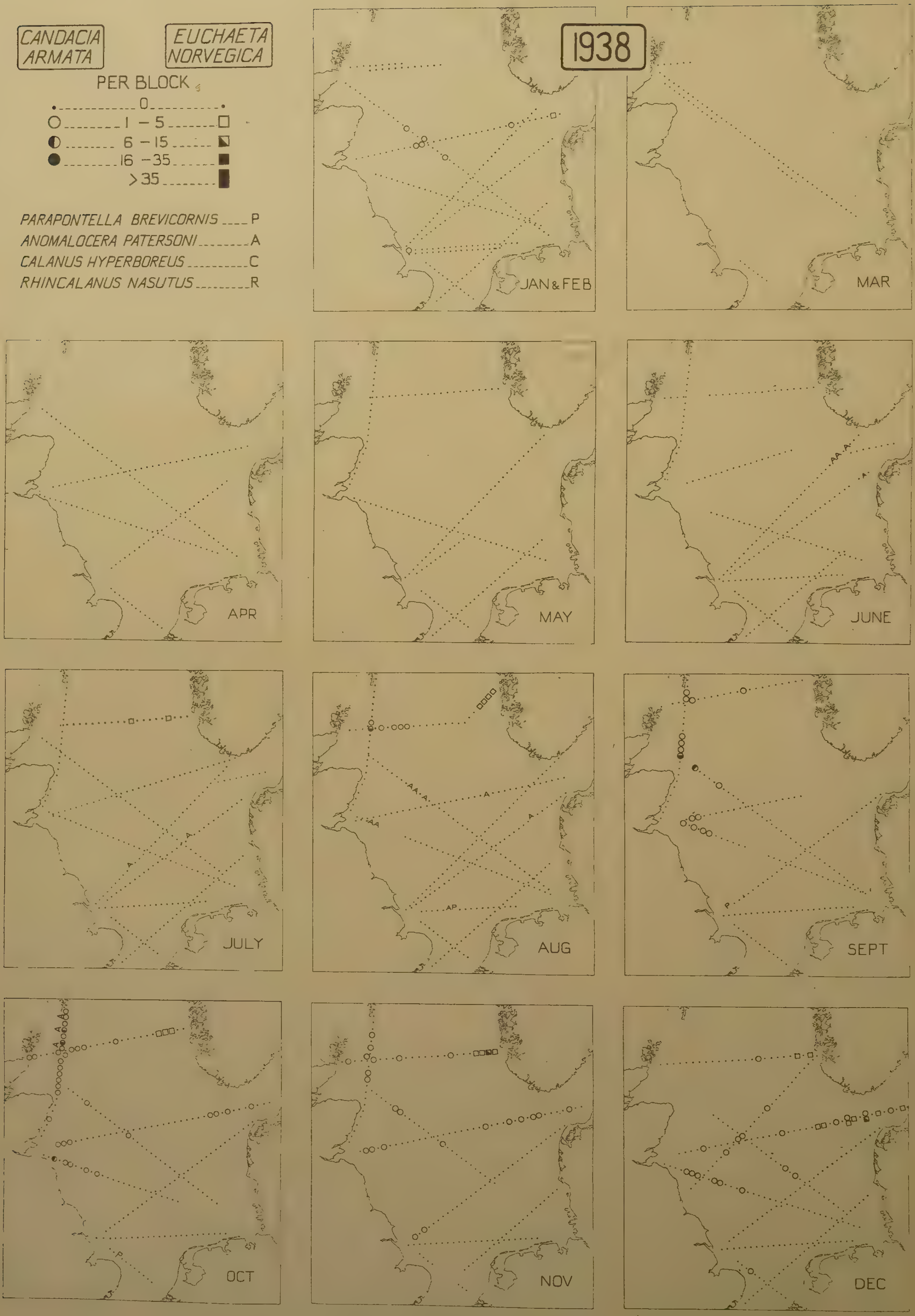
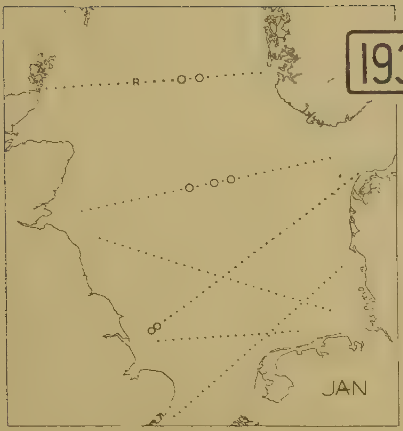
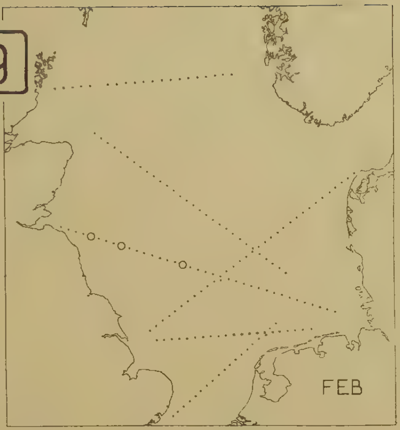

1939
JAN
FEB
MAR
APR
MAY
JUNE
JULY
AUG

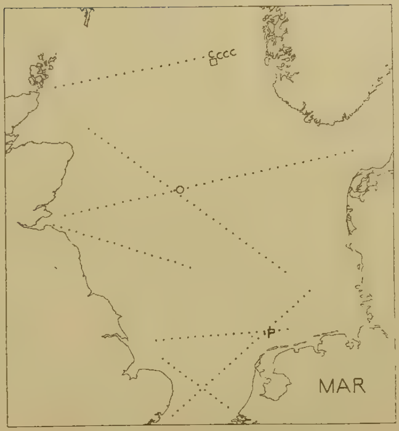
PLATE LXX

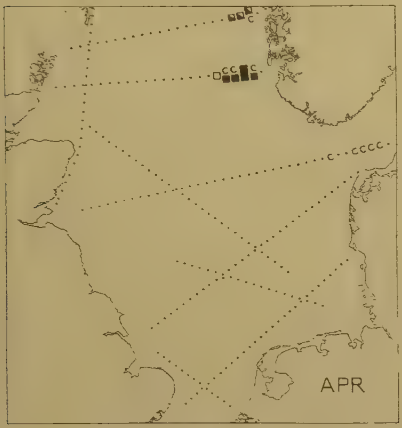

CANDACIA ARMATA
EUCHAETA NORVEGICA
PER BLOCK
• 0 •
○ 1 – 5 □
◐ 6 – 15 ◩
● 16 – 35 ■
>35 ▮
PARAPONTELLA BREVICORNIS P
ANOMALOCERA PATERSONI A
CALANUS HYPERBOREUS C
RHINCALANUS NASUTUS R
1938
JAN & FEB
MAR
APR
MAY
JUNE
JULY
AUG
SEPT
OCT
NOV
DEC

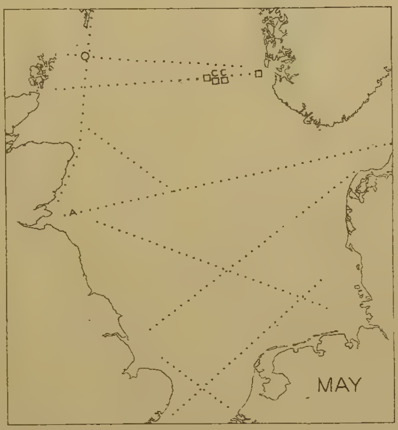
1939

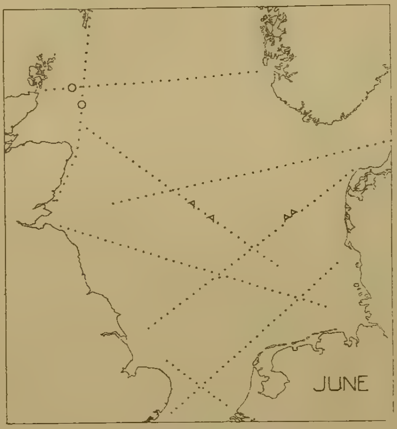


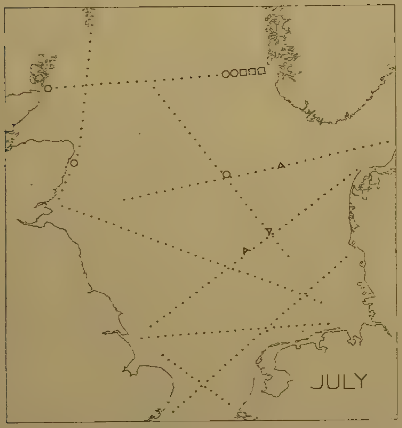


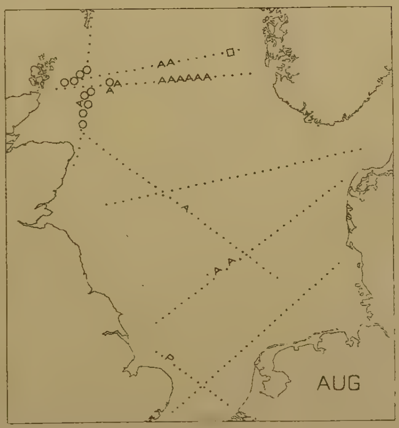



C
C C C
C C C C
APR








A A
A A A A A A
A
A
A A
P
AUG

ISIAS

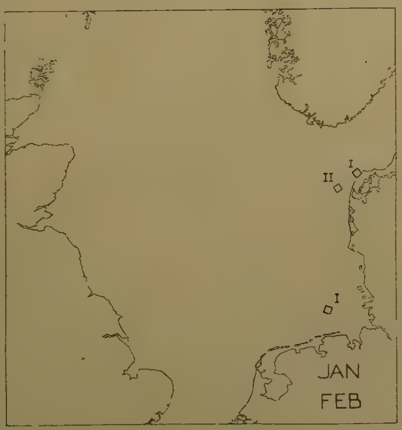
and

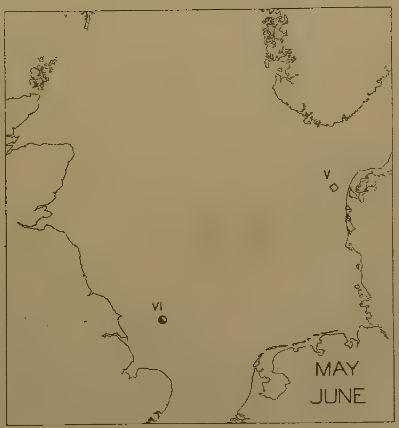
CORYCAEUS

1939

[continued from

Plate LXXII]


I
II
I
JAN
FEB


V
VI
MAY
JUNE

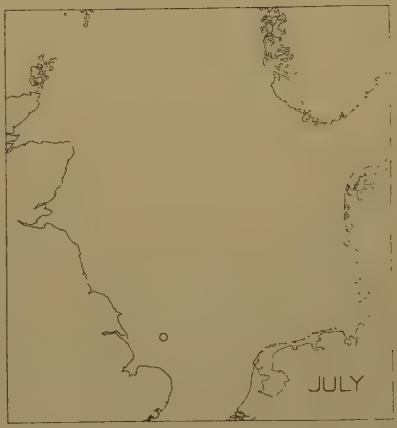
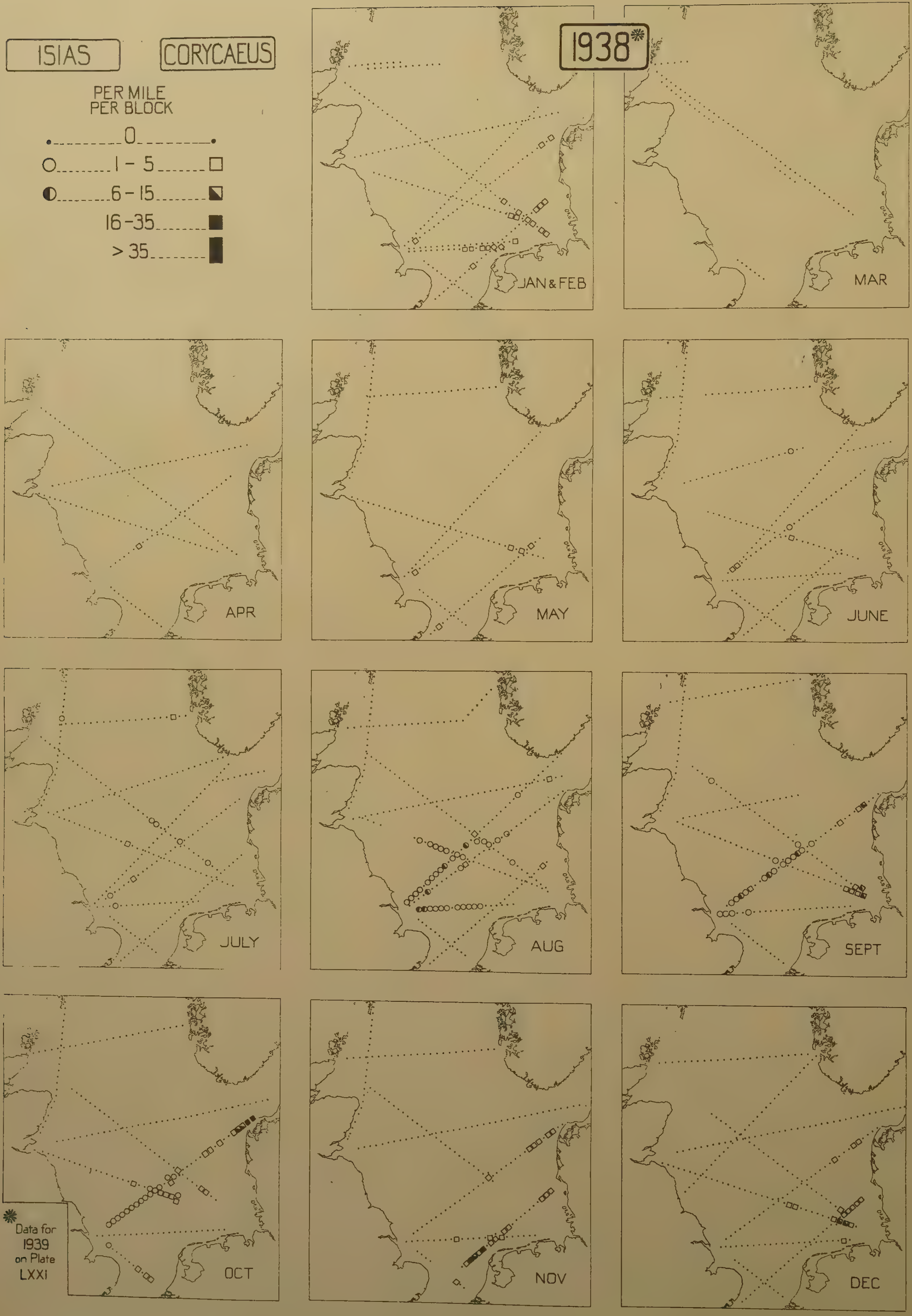
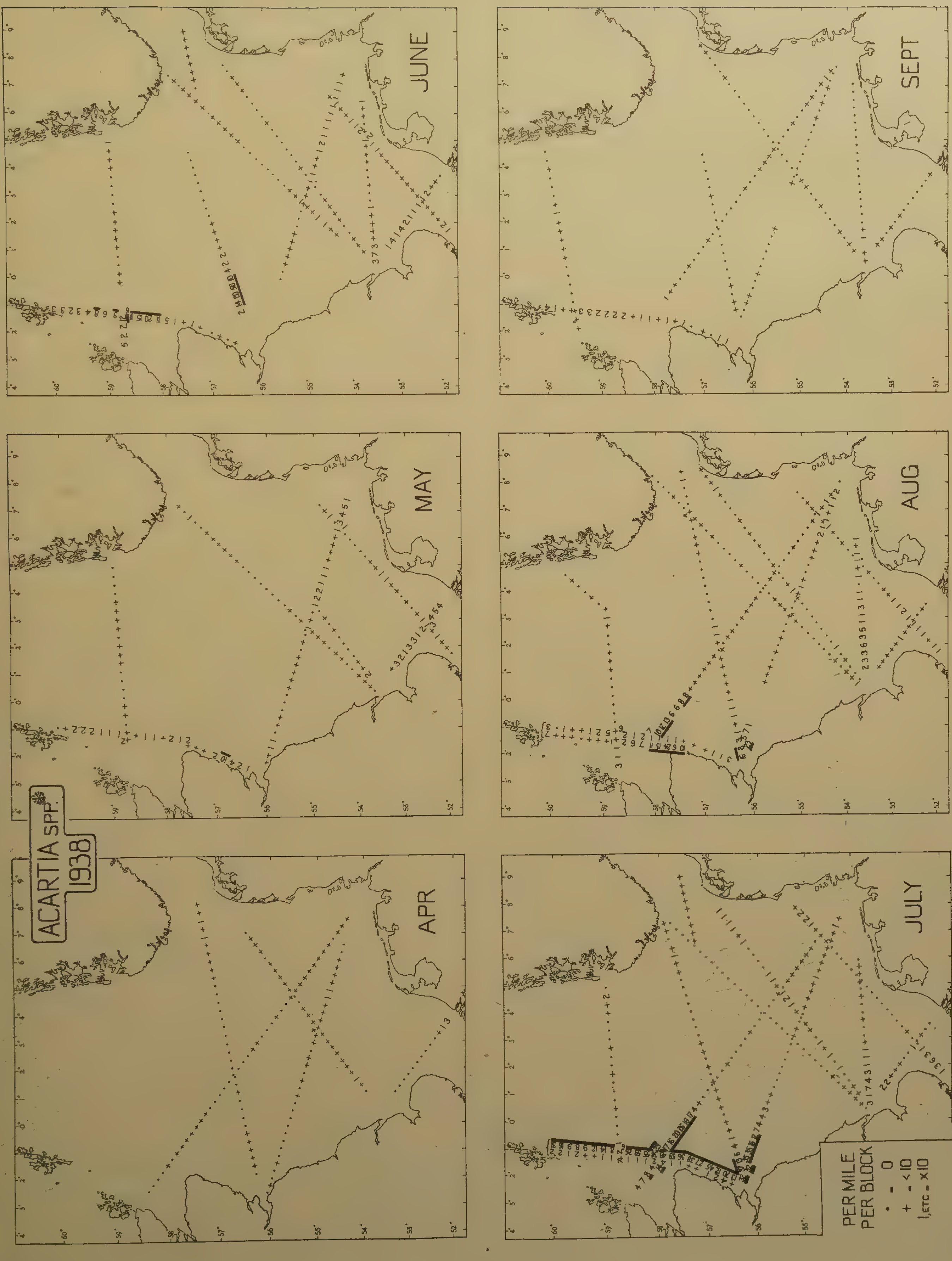


PLATE LXXII


1938*
JAN & FEB
MAR
APR
MAY
JUNE
JULY
AUG
SEPT
OCT
NOV
DEC

ISIAS	PER MILE PER BLOCK	CORYCAEUS
•	0	•
○	1 - 5	□
◐	6 - 15	◪
	16 - 35	■
	> 35	▮

* Data for 1939 on Plate LXXI


ACARTIA SPP.*
1938
APR
MAY
JUNE
JULY
AUG
SEPT
PER MILE
PER BLOCK
· - 0
+ - <10
1, ETC. - x10

* FOR 1939 DATA SEE PLATE LXXXIV

PLATE LXXIV

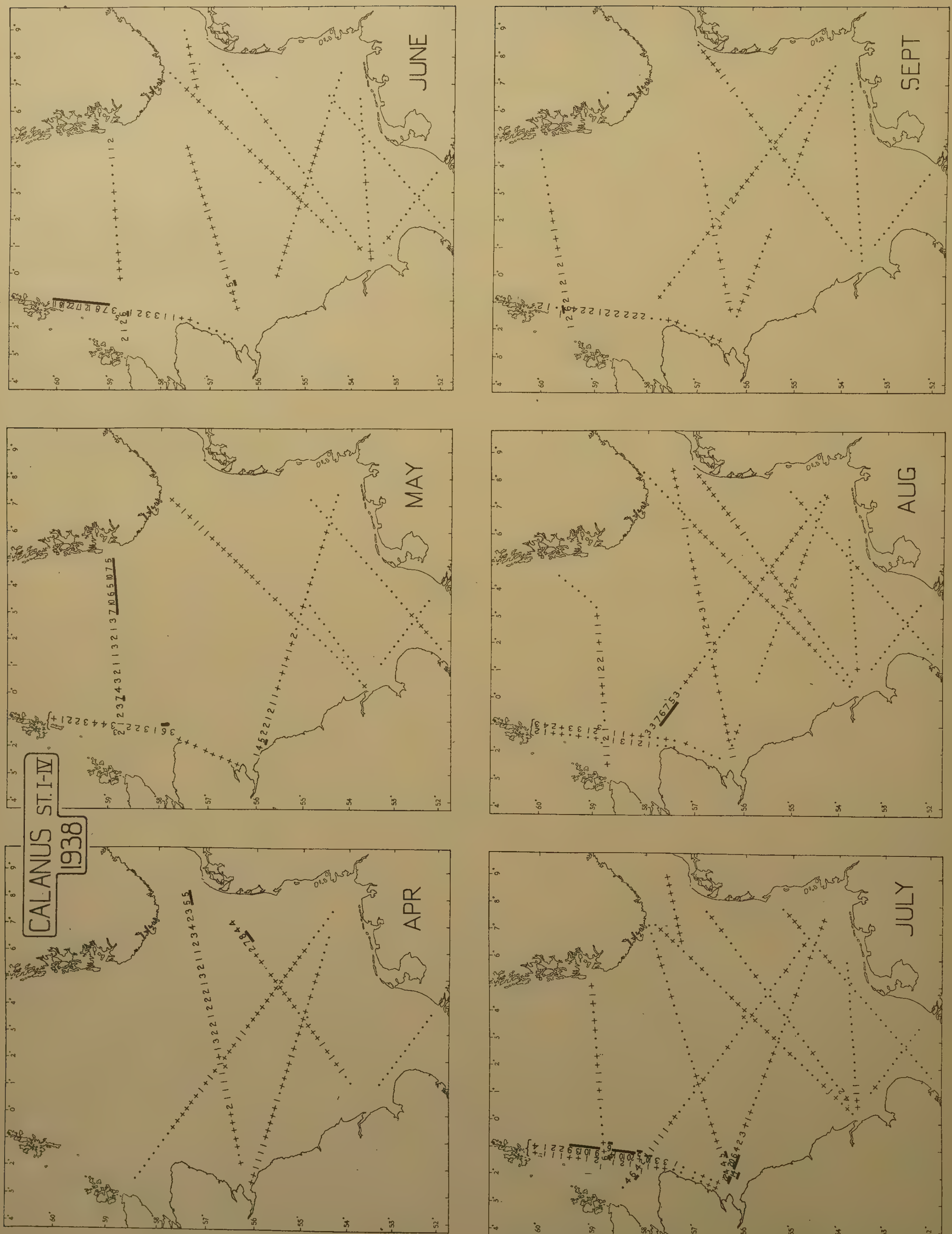
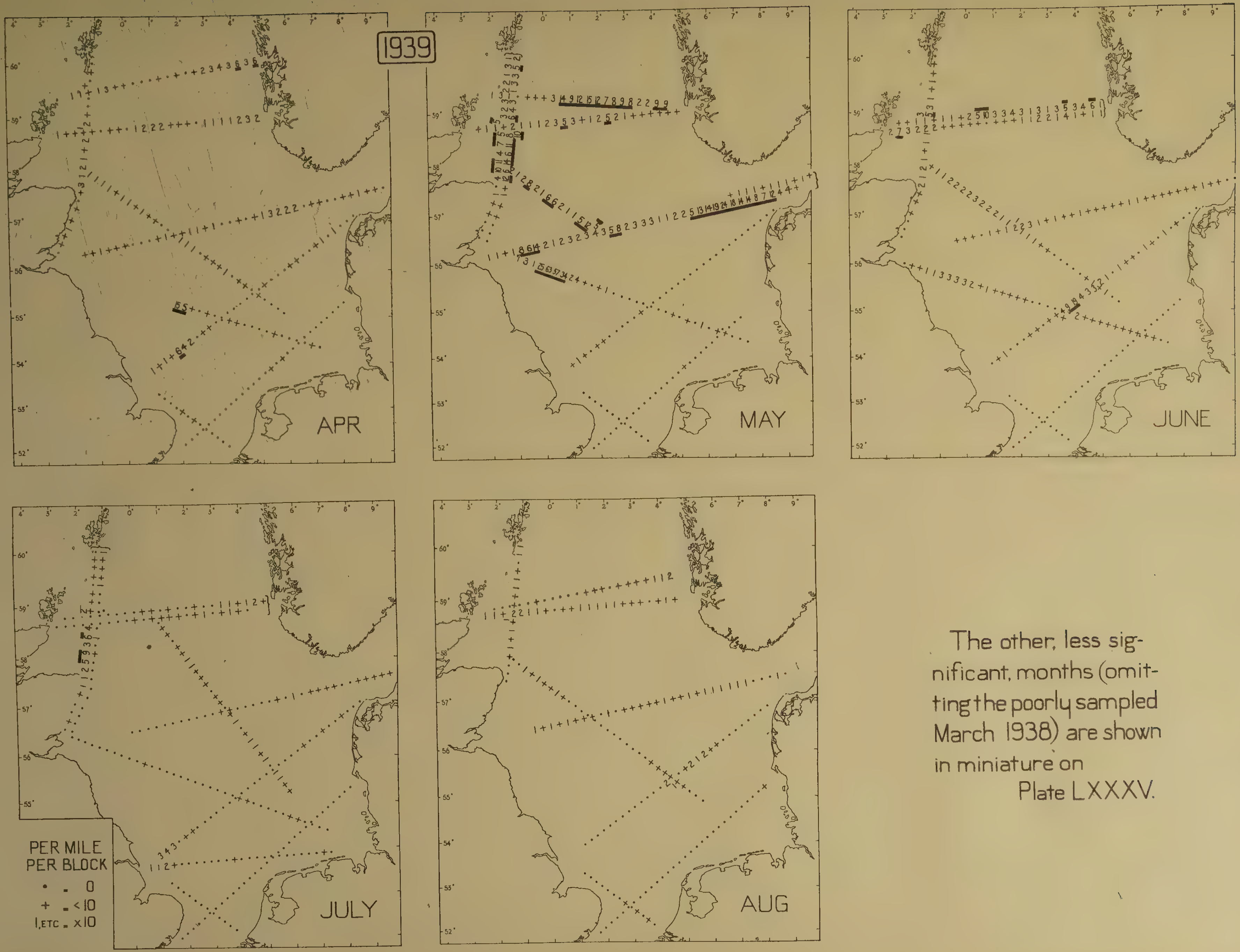
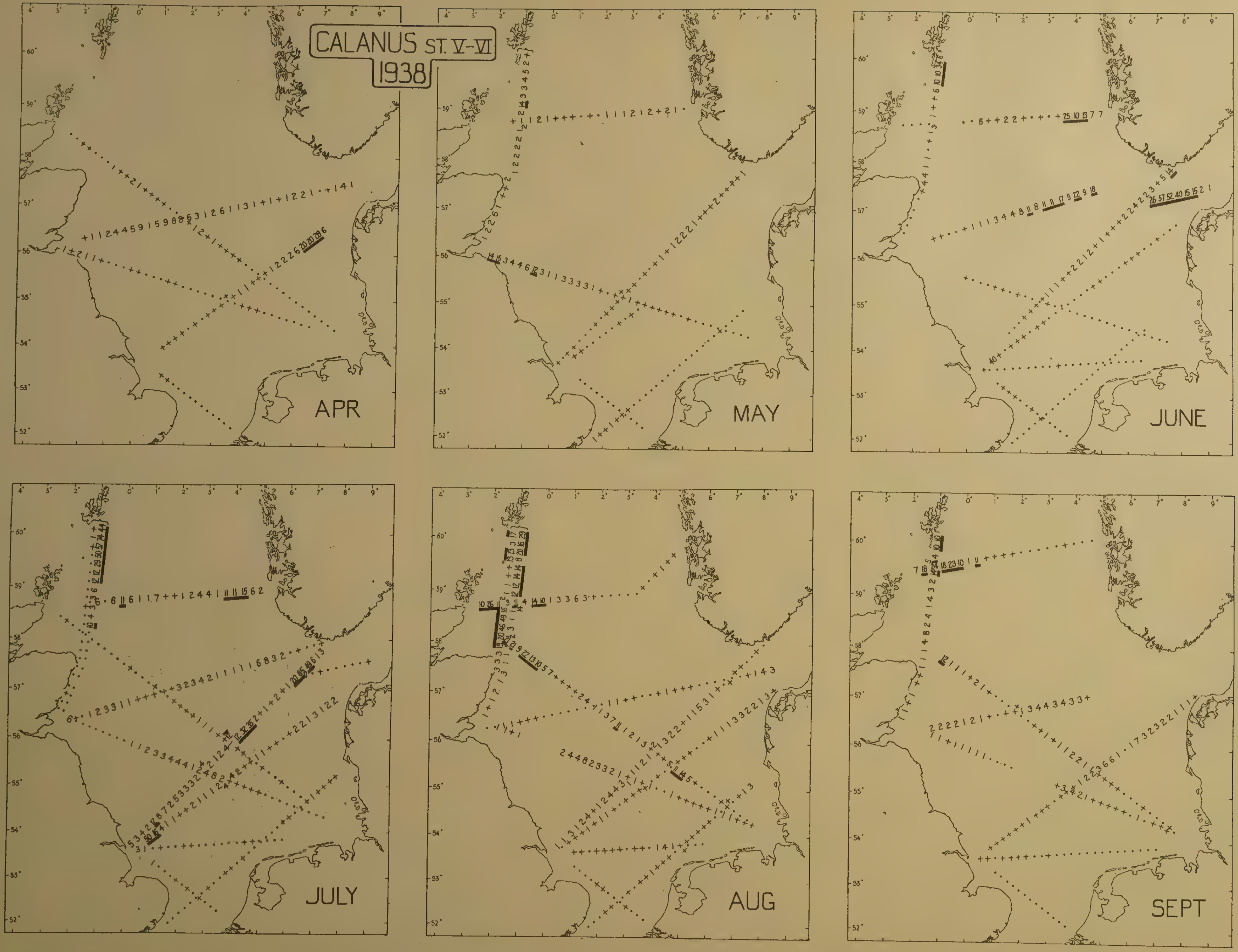

CALANUS ST. I-IV
1938
JUNE
MAY
APR
SEPT
AUG
JULY
60°
59°
58°
57°
56°
55°
54°
53°
52°

PLATE LXXV

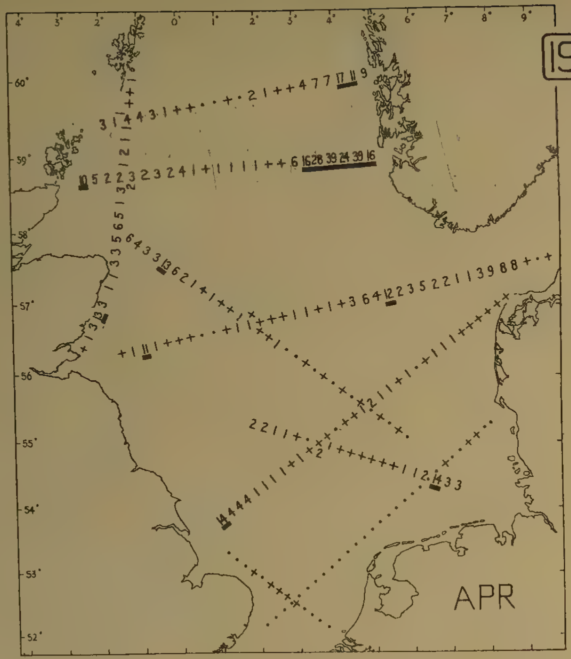

1939
APR
MAY
JUNE
JULY
AUG
PER MILE
PER BLOCK
• - 0
+ - <10
1, ETC - x10

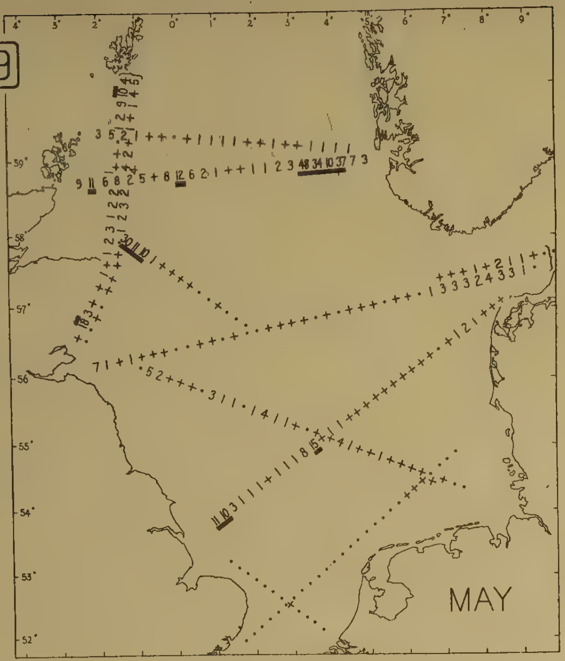
The other, less significant, months (omitting the poorly sampled March 1938) are shown in miniature on Plate LXXXV.

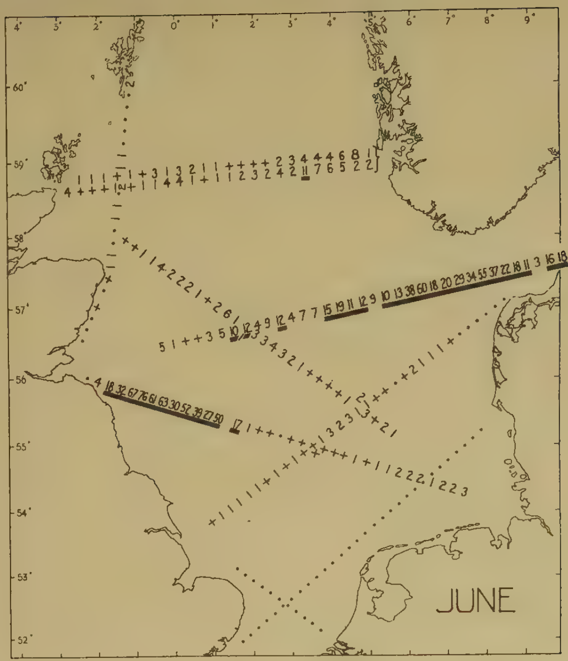
PLATE LXXVI

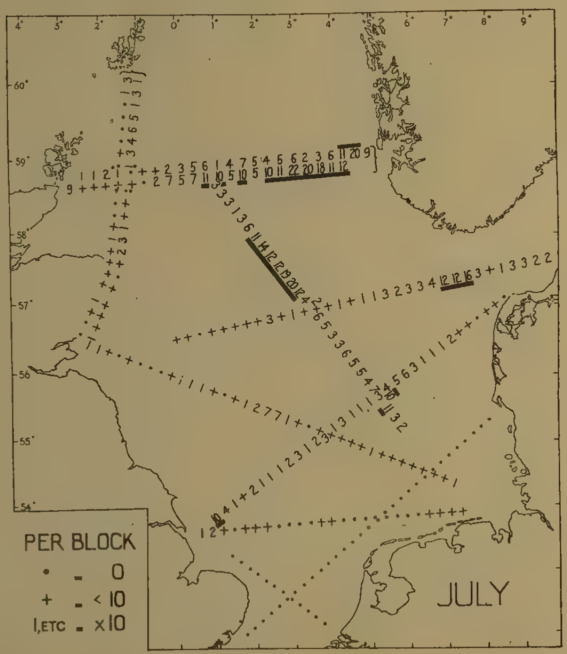

CALANUS ST. V–VI
1938
APR
MAY
JUNE
JULY
AUG
SEPT

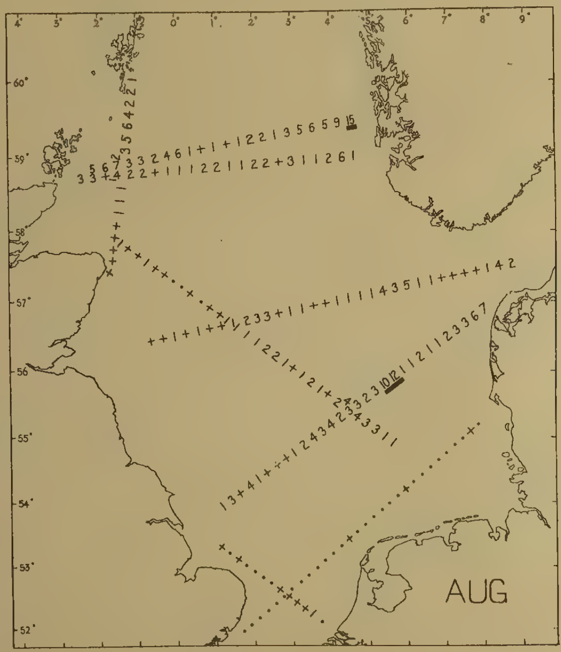
1939








JULY
PER BLOCK
• ‒ 0
+ ‒ < 10
1, ETC ▬ ×10



The other, less significant, months (omitting the poorly sampled March 1938) are shown in miniature on Plate LXXXV.

PLATE LXXVIII

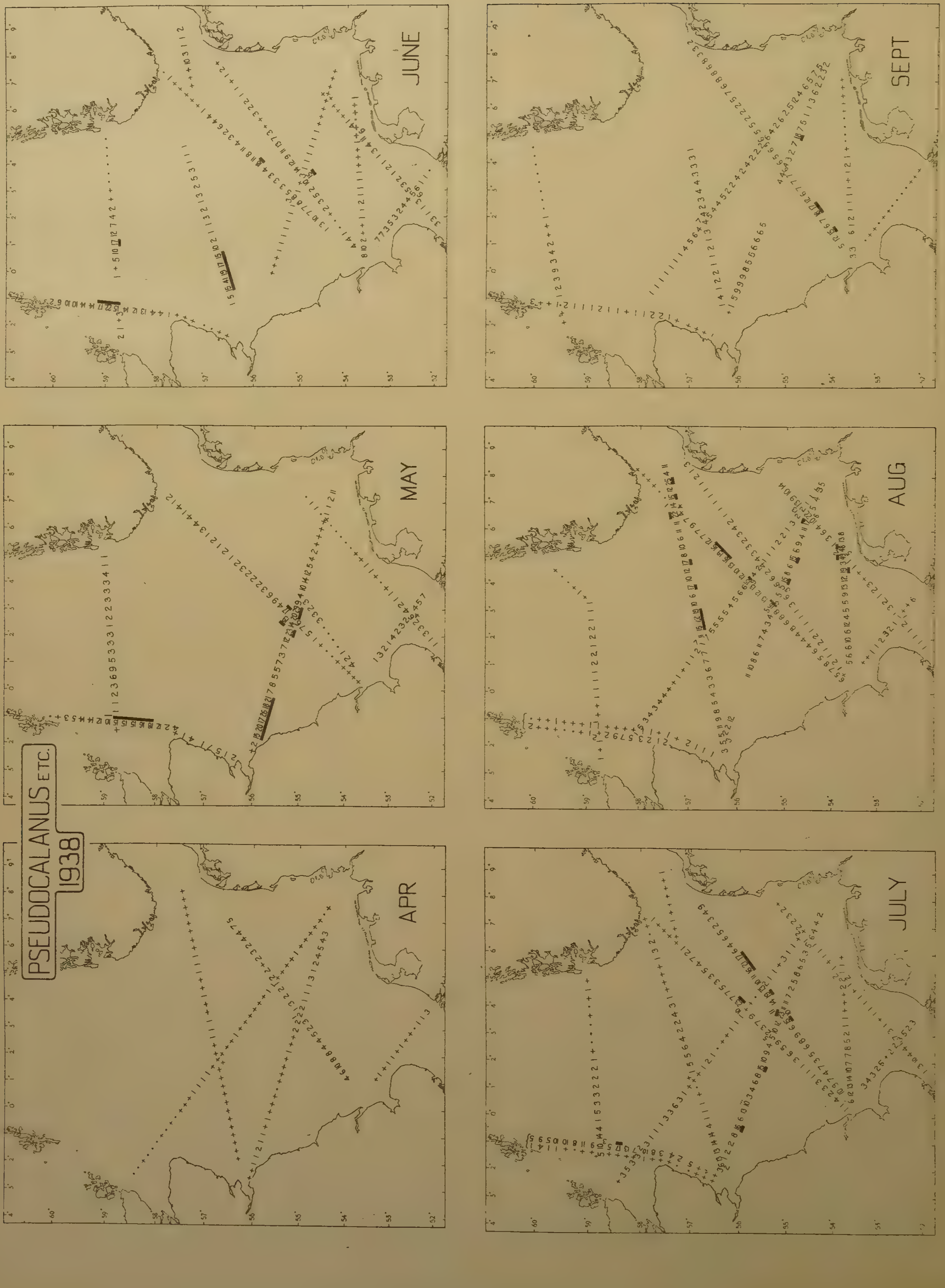
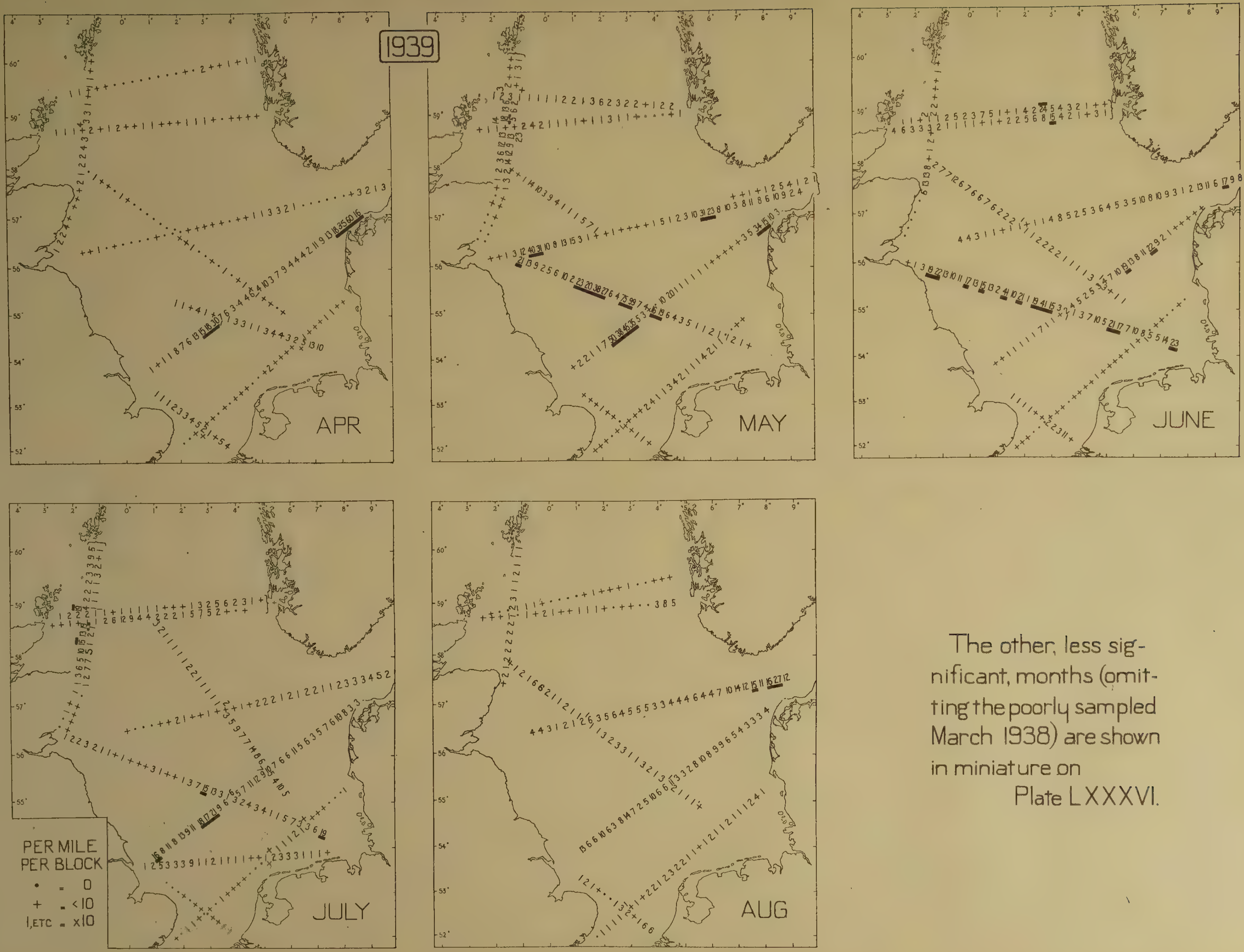

PSEUDOCALANUS ETC.
1938
JUNE
SEPT
MAY
AUG
APR
JULY

PLATE LXXIX


1939
APR
MAY
JUNE
JULY
AUG
PER MILE
PER BLOCK
• = 0
+ = <10
1,ETC = x10

The other, less significant, months (omitting the poorly sampled March 1938) are shown in miniature on Plate LXXXVI.

PLATE LXXX

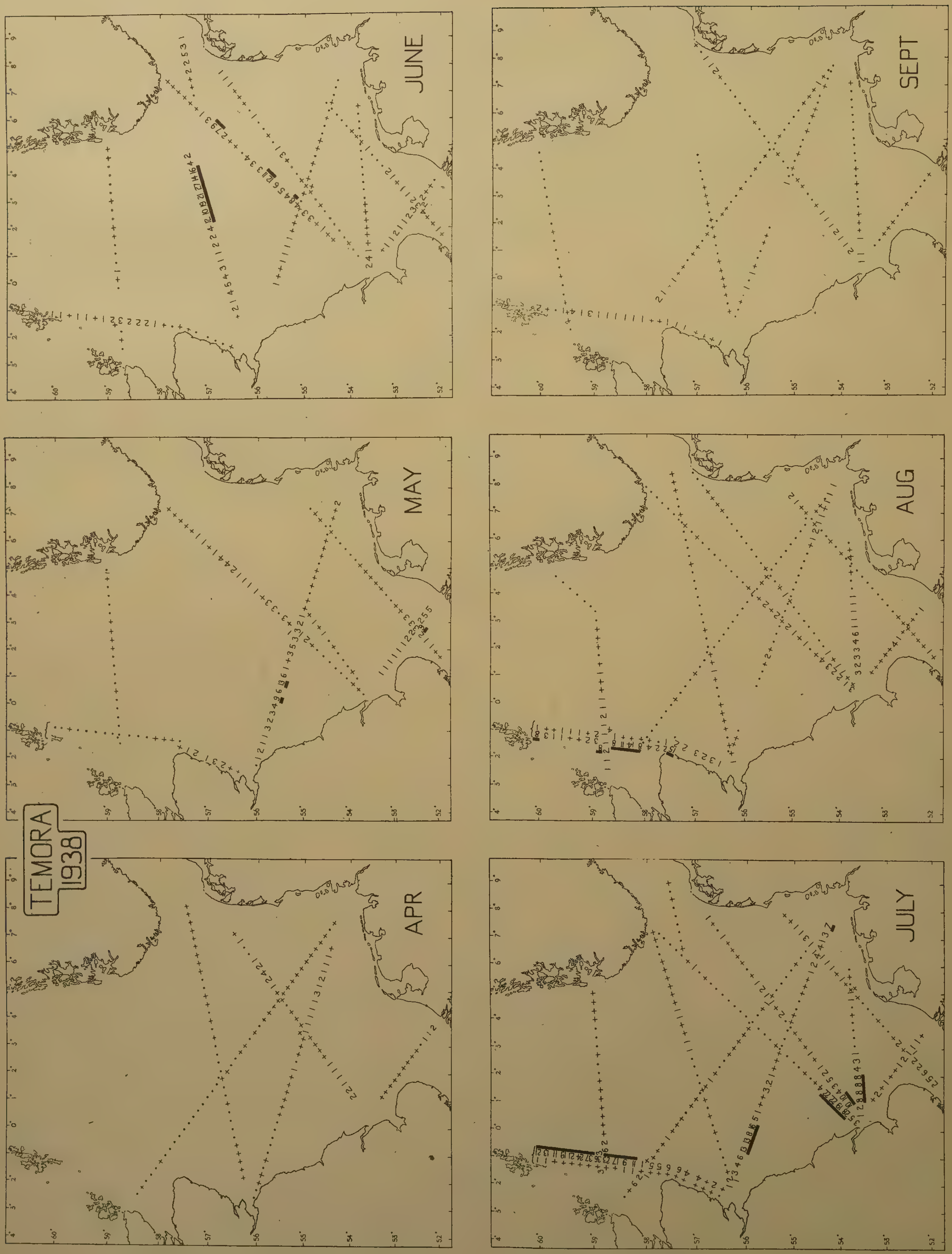
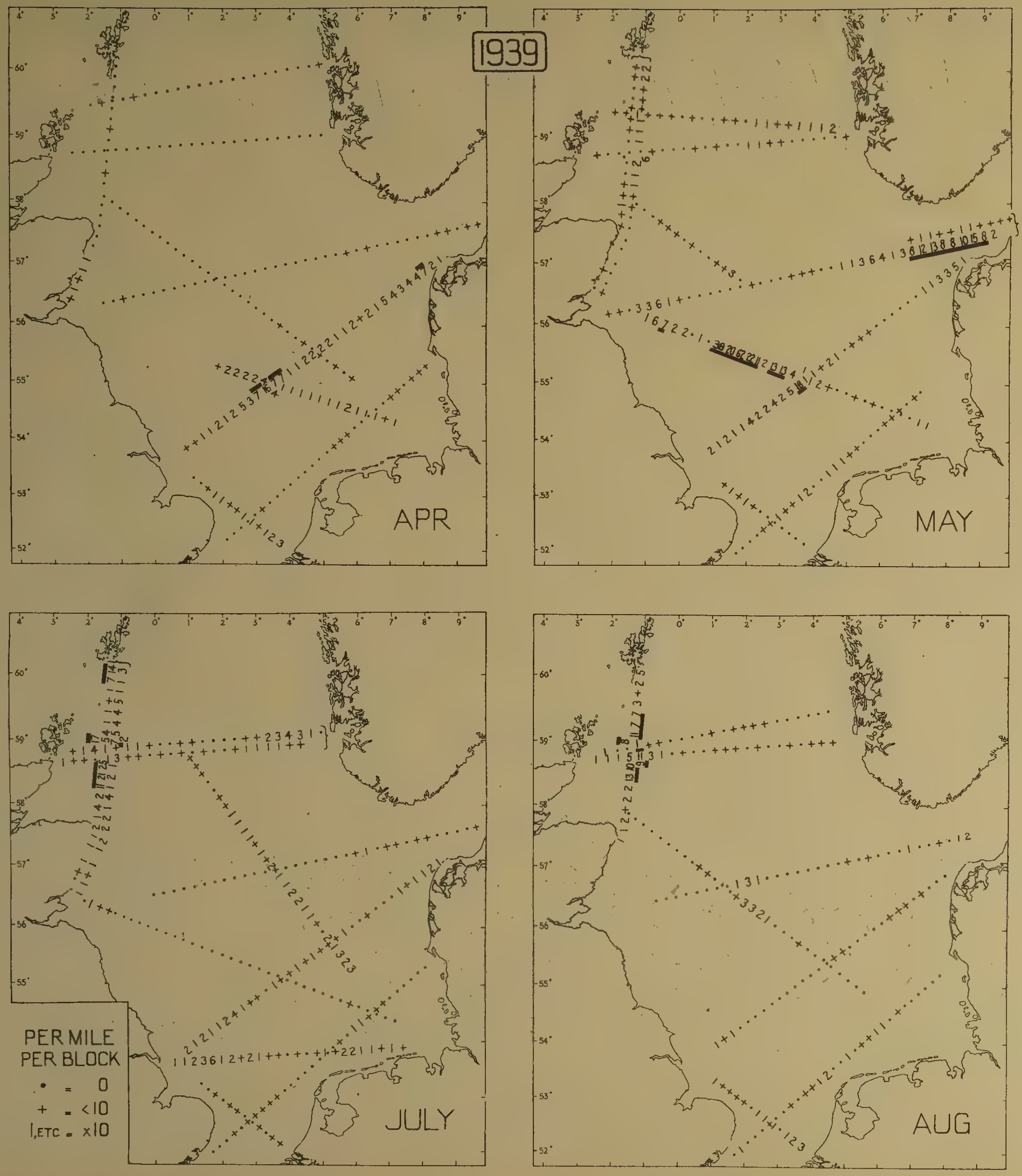
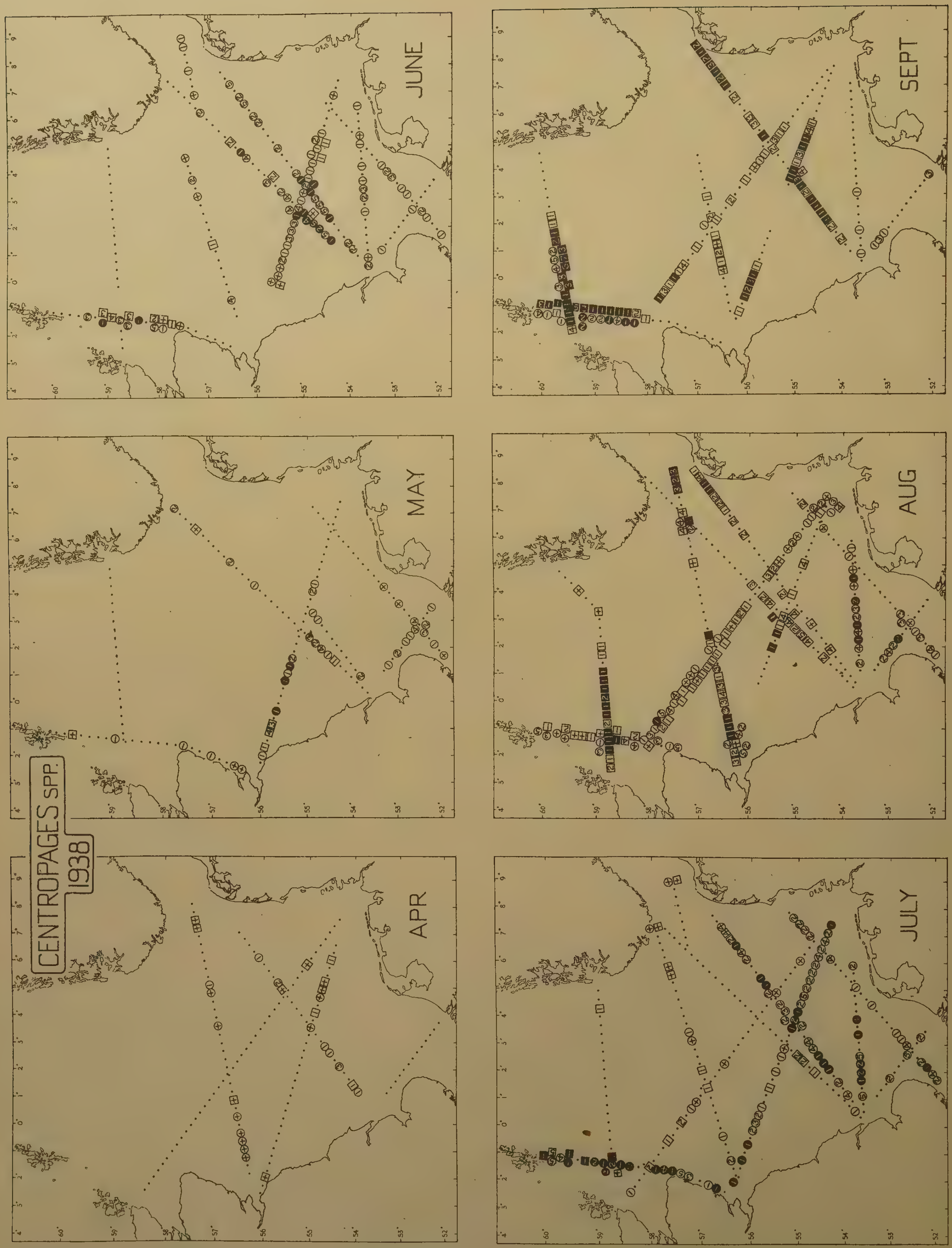

TEMORA
1938
APR
MAY
JUNE
JULY
AUG
SEPT
60°
59°
58°
57°
56°
55°
54°
53°
52°
4°
3°
2°
1°
0°
1°
2°
3°
4°
5°
6°
7°
8°
9°

PLATE LXXXI

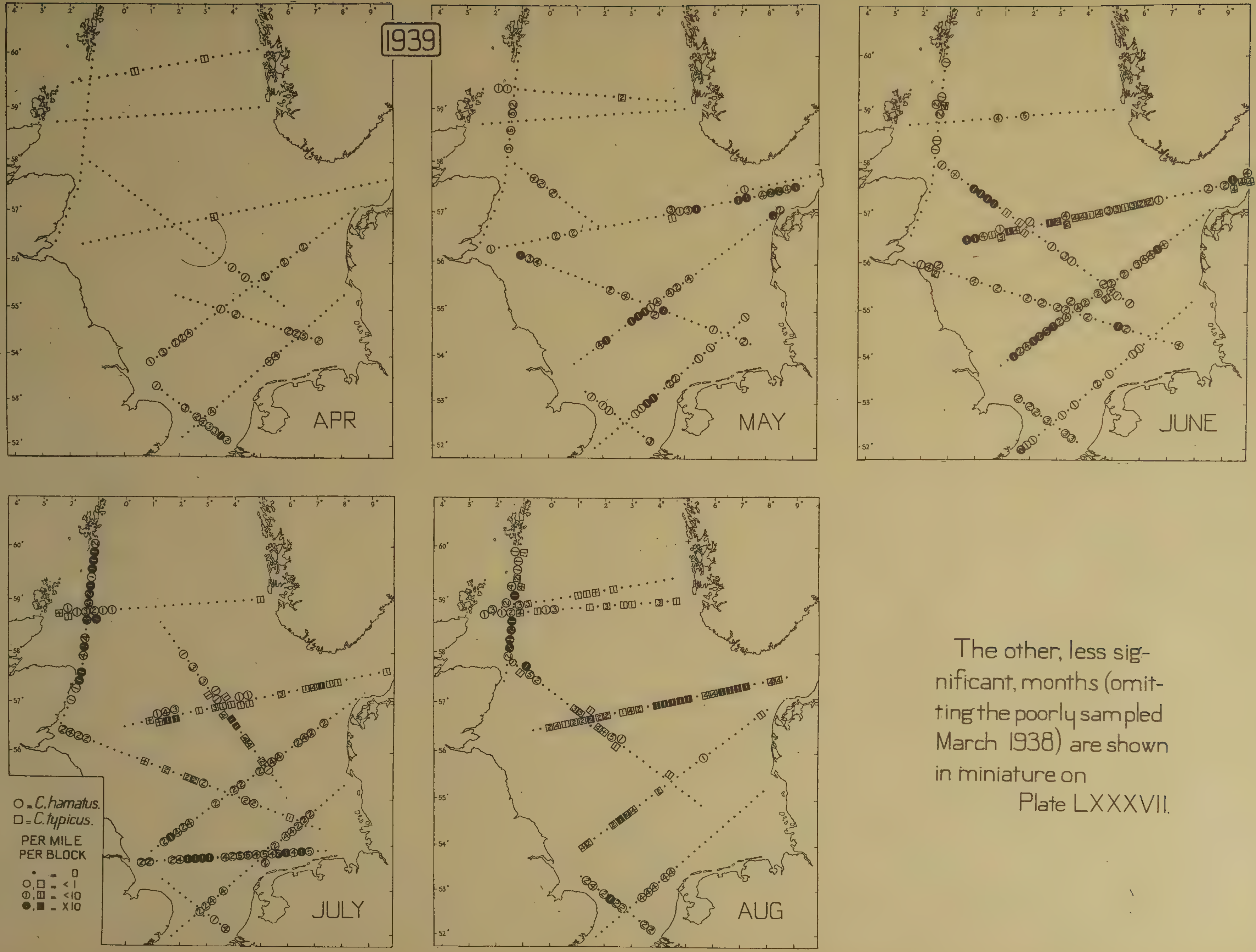

1939
APR
MAY
JUNE
JULY
AUG
PER MILE
PER BLOCK
• = 0
+ - <10
I,ETC ▬ x10

The other, less significant, months (omitting the poorly sampled March 1938) are shown in miniature on Plate LXXXVI.

PLATE LXXXII

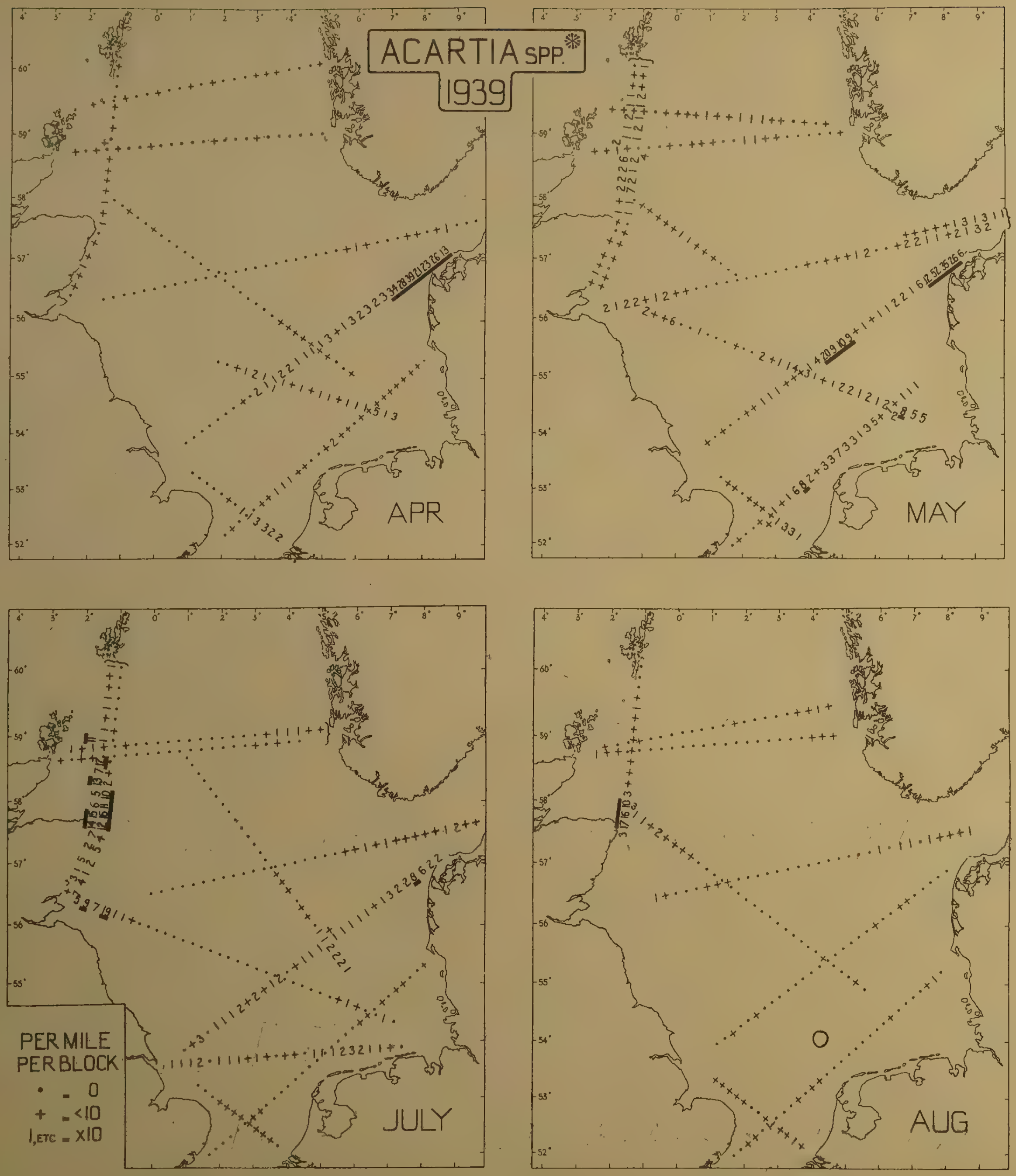

JUNE
SEPT
MAY
AUG
APR
JULY
60°
59°
58°
57°
56°
55°
54°
53°
52°

CENTROPAGES SPP.
1938


1939
APR
MAY
JUNE
JULY
AUG
O = C. hamatus.
□ = C. typicus.
PER MILE
PER BLOCK
• ▬ = 0
O,□ = <1
Ⓘ,◫ = <10
●,■ = X10

The other, less significant, months (omitting the poorly sampled March 1938) are shown in miniature on Plate LXXXVII.

PLATE LXXXIV



ACARTIA SPP.*
1939

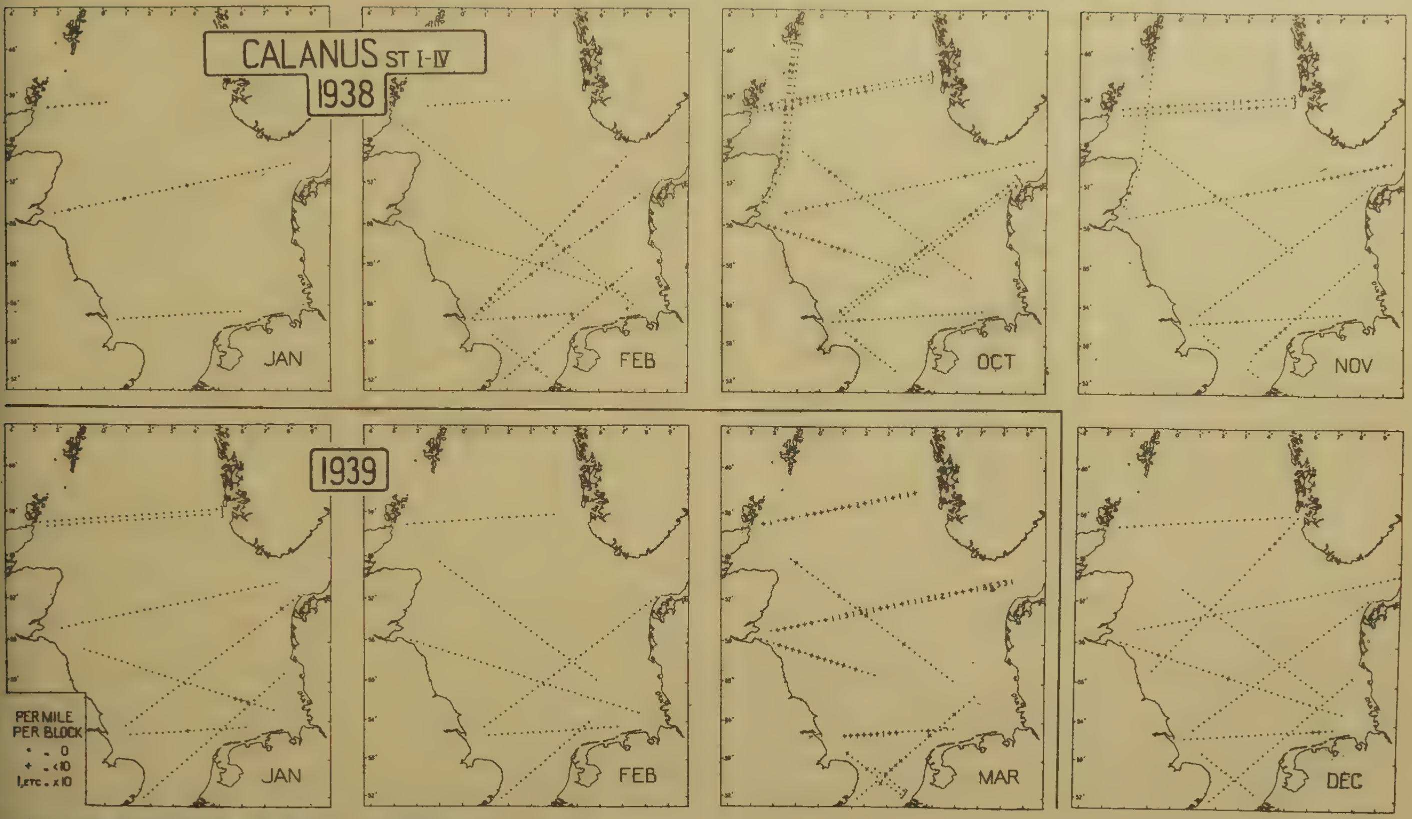
APR
MAY
JUNE
JULY
AUG
PER MILE
PER BLOCK
• = 0
+ = <10
1, ETC = X10

The other, less significant, months (omitting the poorly sampled March 1938) are shown in miniature on Plate LXXXVII.

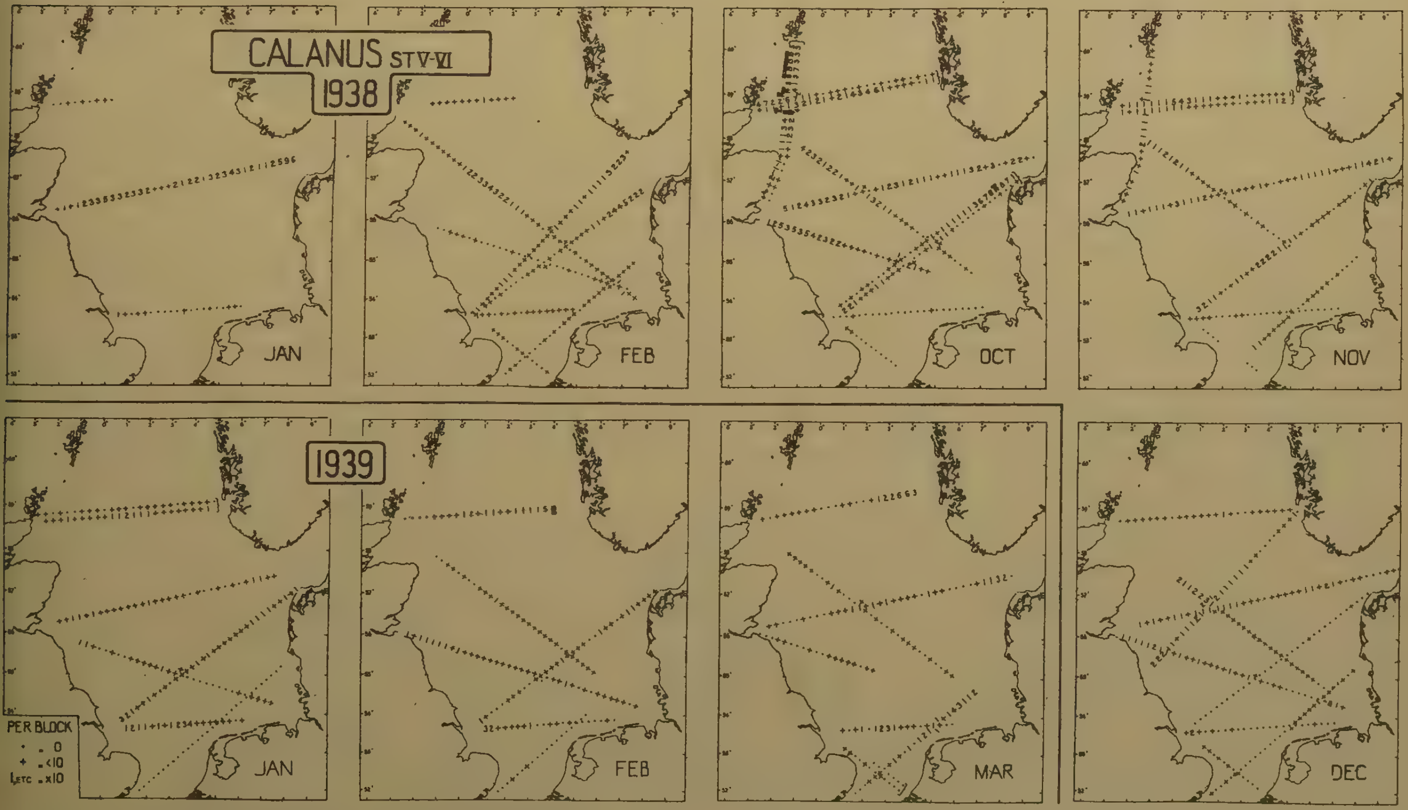
* FOR 1938 DATA SEE PLATE LXXIII

PLATE LXXXV

FOR USE WITH LENS


CALANUS ST I-IV
1938
JAN
FEB
OCT
NOV
1939
JAN
FEB
MAR
DEC
PER MILE
PER BLOCK
• - 0
+ - <10
I, ETC - x10

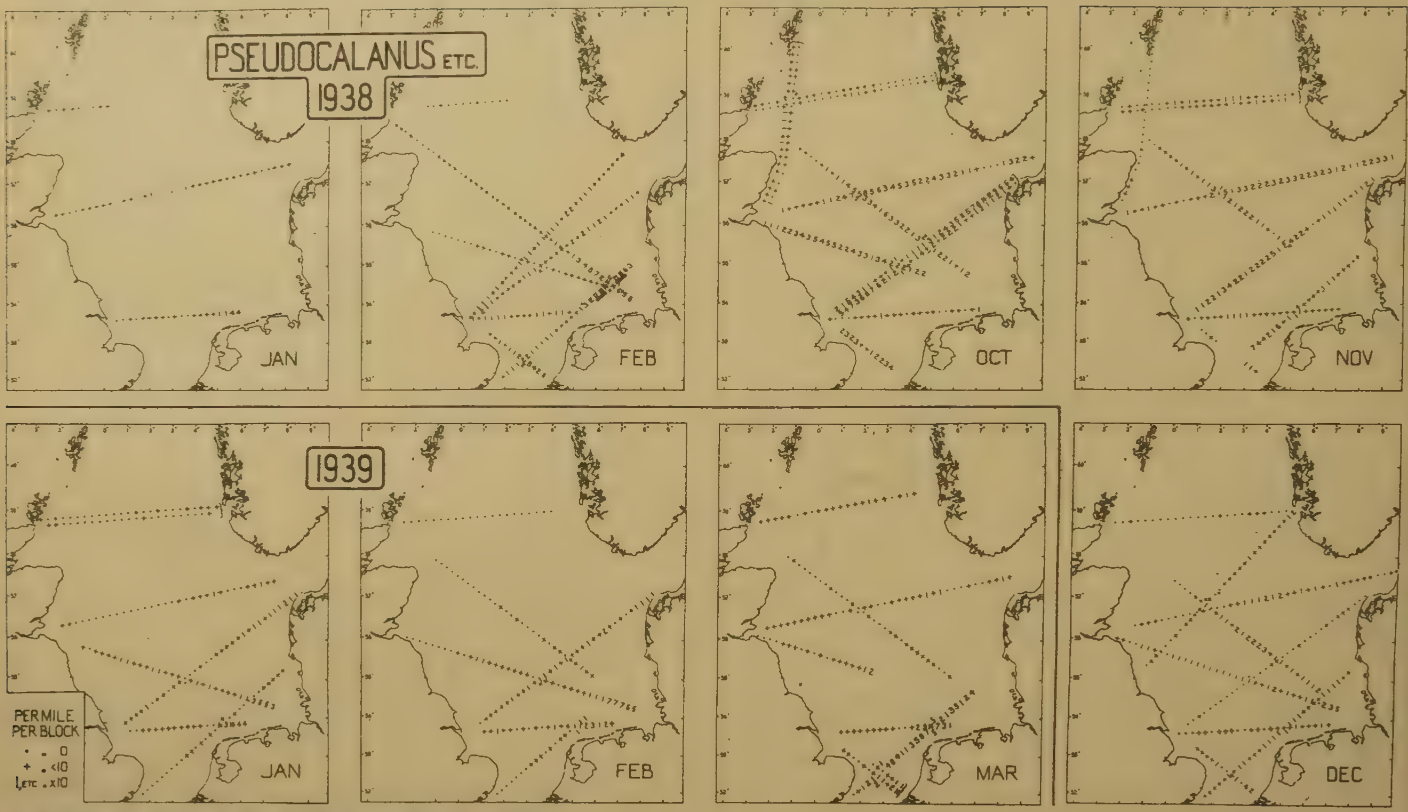
WINTER DATA FOR PLATES LXXIV AND LXXV


CALANUS ST V-VI
1938
JAN
FEB
OCT
NOV
1939
JAN
FEB
MAR
DEC
PER BLOCK
• - 0
+ - <10
I, ETC - x10

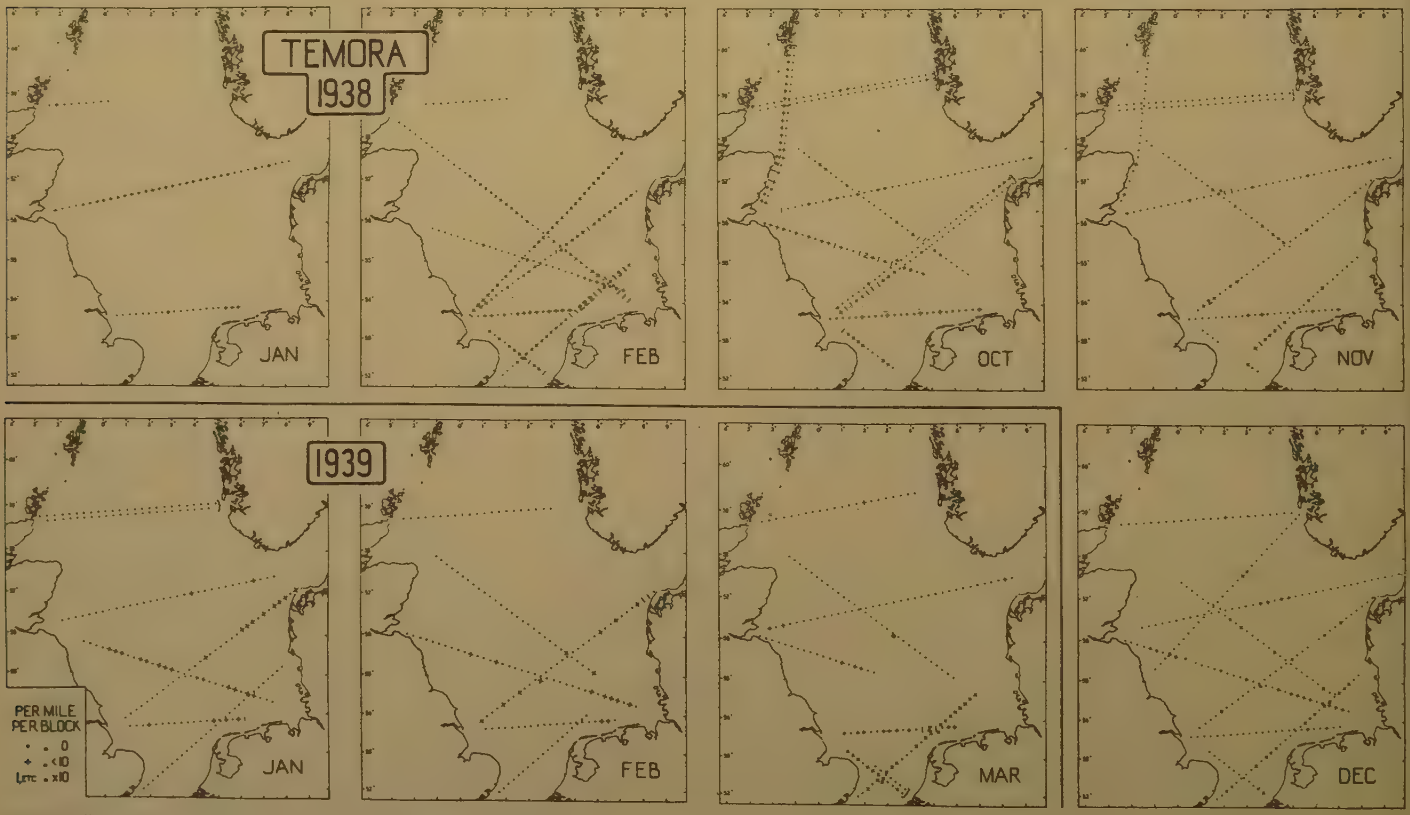
WINTER DATA FOR PLATES LXXVI AND LXXVII

PLATE LXXXVI

FOR USE WITH LENS


PSEUDOCALANUS ETC.
1938
JAN
FEB
OCT
NOV
1939
PER MILE
PER BLOCK
• - 0
+ . <10
|ETC . x10
JAN
FEB
MAR
DEC

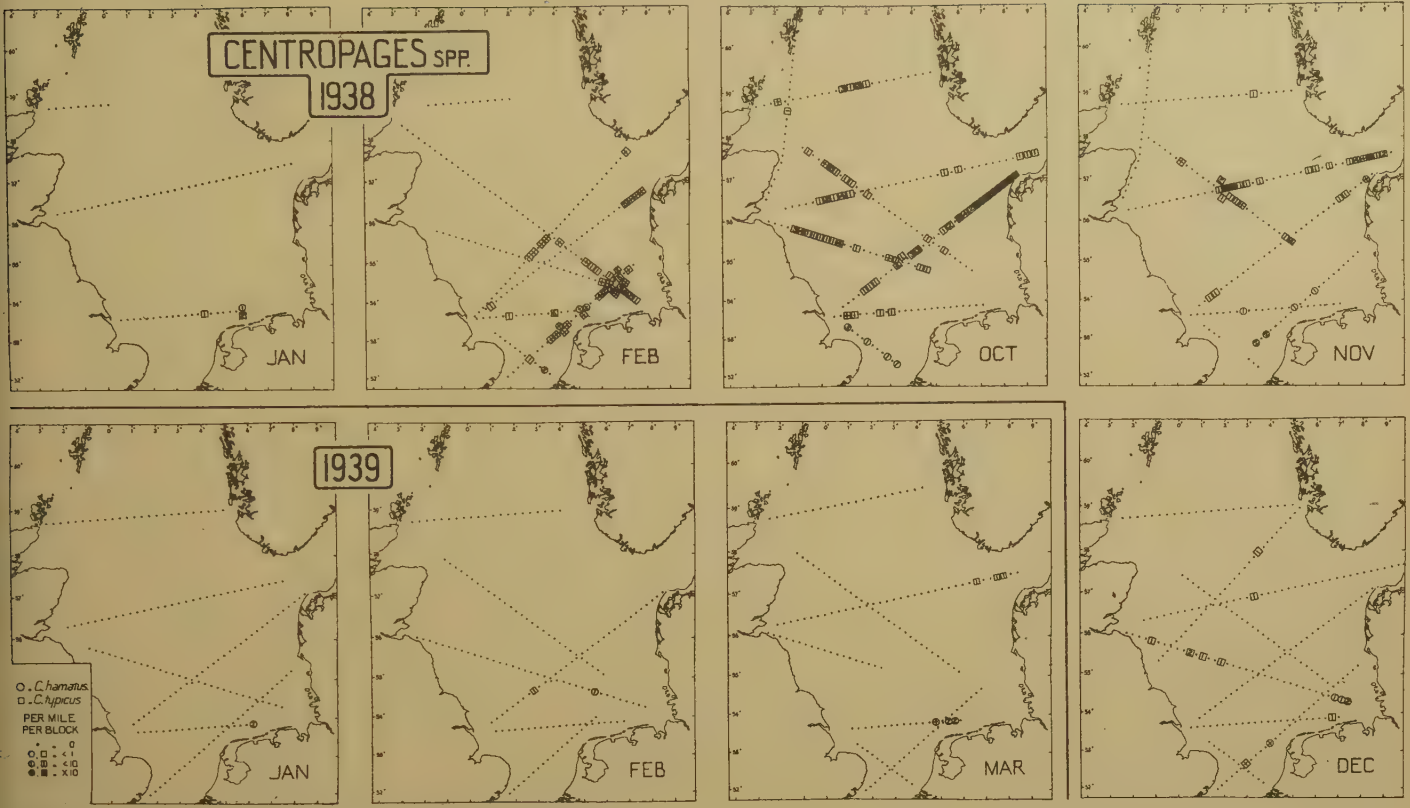
WINTER DATA FOR PLATES LXXVIII AND LXXIX


TEMORA
1938
JAN
FEB
OCT
NOV
1939
PER MILE
PER BLOCK
• - 0
+ . <10
|ETC . x10
JAN
FEB
MAR
DEC

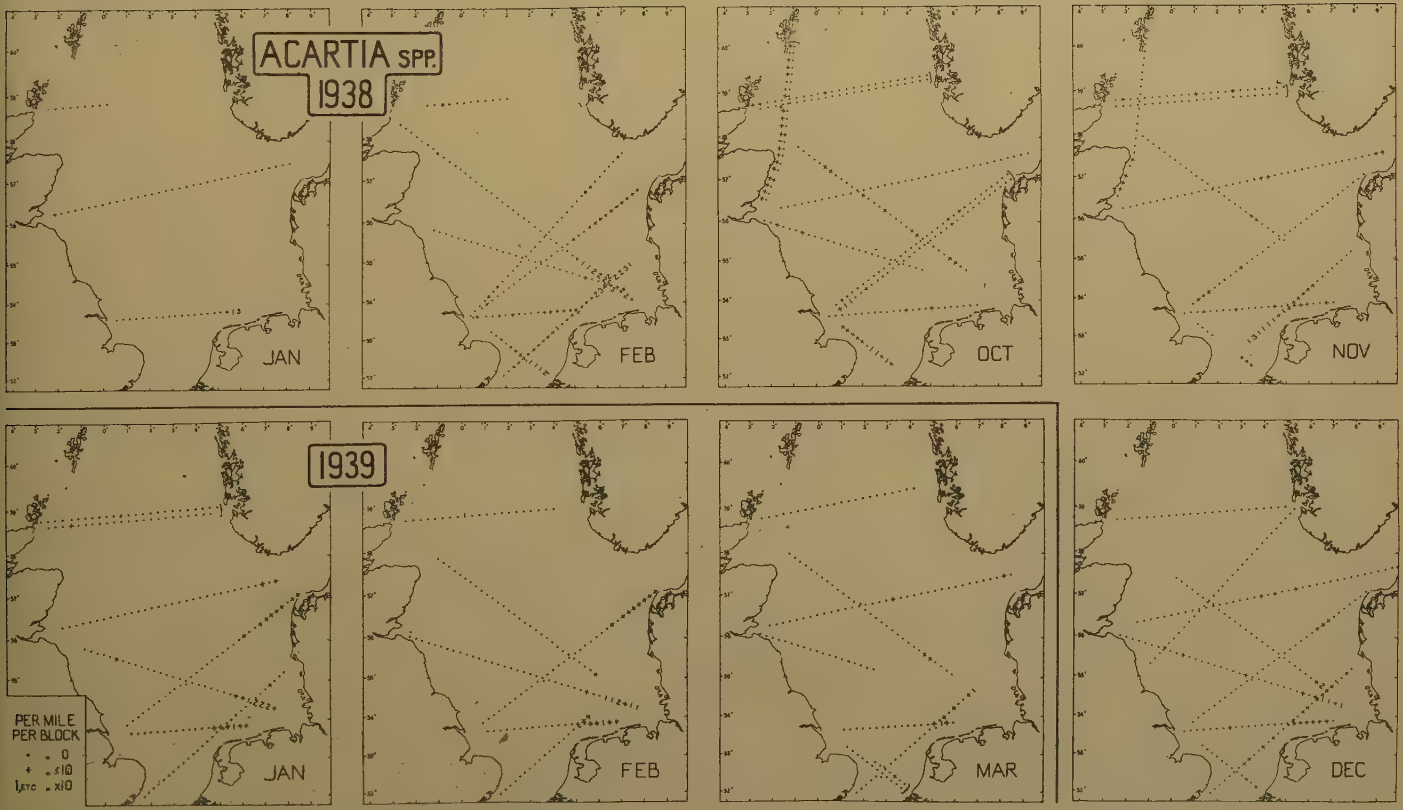
WINTER DATA FOR PLATES LXXX AND LXXXI

PLATE LXXXVII

FOR USE WITH LENS


CENTROPAGES SPP.
1938
JAN
FEB
OCT
NOV
1939
JAN
FEB
MAR
DEC
○ . *C. hamatus.*
□ . *C. typicus*
PER MILE
PER BLOCK
• . 0
○, □ . < 1
◐, ◨ . < 10
●, ■ . × 10

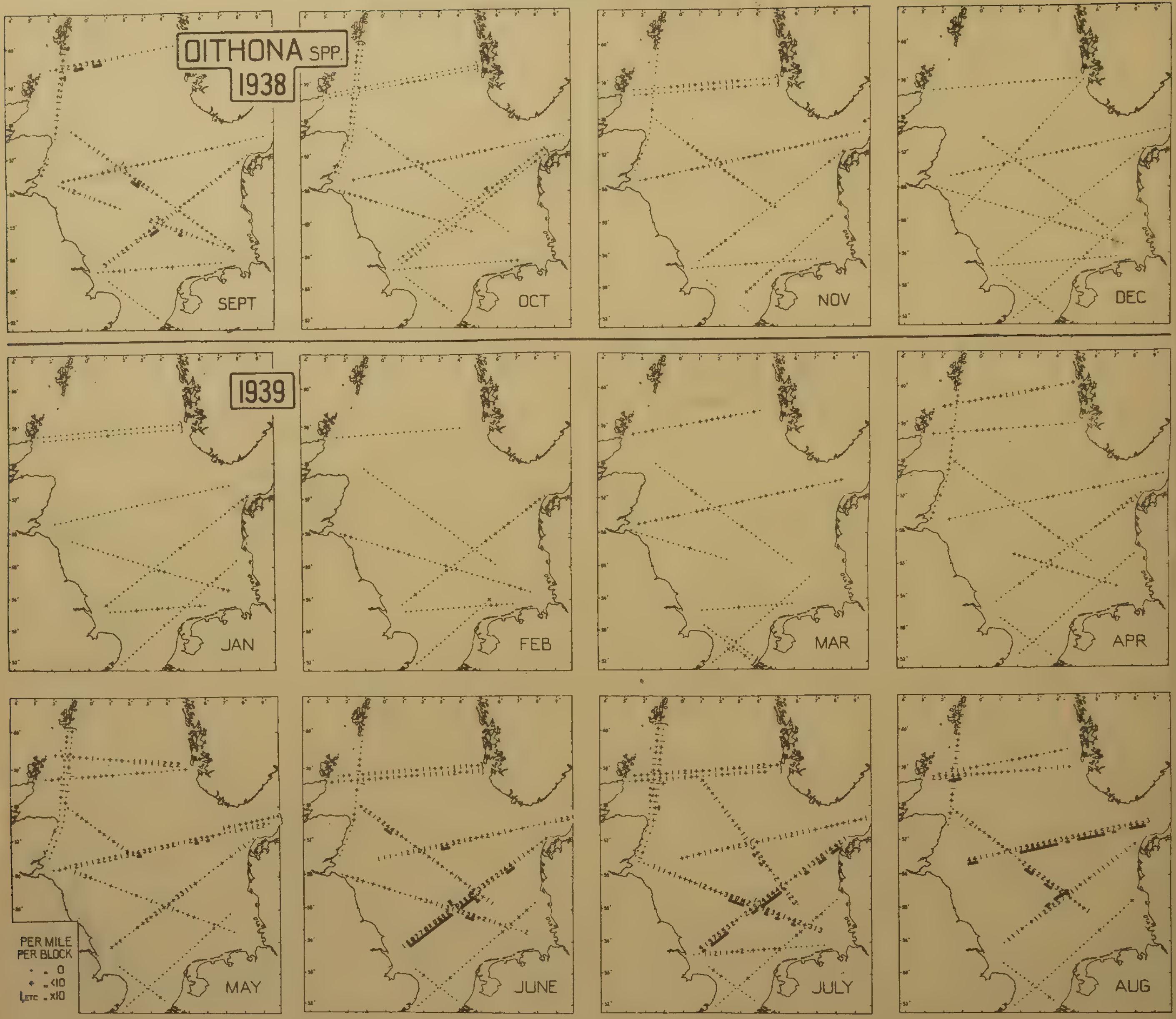
WINTER DATA FOR PLATES LXXXII AND LXXXIII


ACARTIA SPP.
1938
JAN
FEB
OCT
NOV
1939
JAN
FEB
MAR
DEC
PER MILE
PER BLOCK
• . 0
+ . ≤10
1, ETC . ×10

WINTER DATA FOR PLATES LXXIII AND LXXXIV

PLATE LXXXVIII

FOR USE WITH LENS


OITHONA SPP.
1938
SEPT
OCT
NOV
DEC
1939
JAN
FEB
MAR
APR
MAY
JUNE
JULY
AUG
PER MILE
PER BLOCK
· - 0
+ - <10
⌊ETC - x10

[*Hull Bulletins of Marine Ecology, No. 12, Vol. II, pp.* 133–171, *June, 1948.*]

CONTINUOUS PLANKTON RECORDS:

SIZE VARIATIONS IN DIATOMS AND THEIR ECOLOGICAL SIGNIFICANCE

BY

C. E. LUCAS, D.Sc.,

AND

H. G. STUBBINGS, M.A., Ph.D.

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INTRODUCTION.

Savage and Wimpenny (1936) first suggested using the size-variations of marine diatoms, for distinguishing the different diatom "patches" in the sea, and Wimpenny (1936) considered them in relation to their environment. Garstang (1937) re-examined Wimpenny's data for *Rhizosolenia styliformis* Brightwell in the light of the auxospore cycle, and emphasized the possible value of "continuous recording" of diatom sizes in relation to water movements. Re-examination of the earlier records of *Rhizosolenia styliformis* in this laboratory had, in fact, already begun, and from the beginning of 1938 measurements were made regularly during the routine analysis of all records. In view of the preliminary results, measurements were also made later of *Biddulphia sinensis* Greville. We should like here to express our appreciation of the work done by our colleague, Mr. W. Macnae, who assisted in the routine analysis before he left the Department in 1939.

Rhizosolenia styliformis BRIGHTWELL.

Whilst detailed consideration of our data had to be deferred during the war, a brief account was published (Lucas, 1941, p. 43, and Plate VII, 'Bulletin' No. 8) showing how the sizes of Rhizosolenia in 1938 were much smaller in the north-western part of the North Sea than in the south-eastern part, with signs of mixing along the boundary. More recently Wimpenny (1946) reviewed his Southern North Sea measurements over the period 1932–1938, and demonstrated the occurrence of an auxospore cycle with appropriate size variations during that period. In addition, he reconsidered the systematics of this diatom over a wider area. The present material concerns the size variations of *R. styliformis* in the North Sea. Much of it covers similar ground and is in substantial agreement with Mr. Wimpenny's data, so that it can be dealt with briefly. Certain aspects of it, however, are complementary to his data (which he had most kindly communicated to us in advance of publication), and attention will be concentrated on these. The recorded distributions of Rhizosolenia during 1932–1939 have already been published (Lucas, 1940, Plates XXII–XXXVI, and Lucas, 1941, Plates VII–XI). In the light of Wimpenny's discussion of the systematics of *R. styliformis*, we should emphasize that, in our work, we regarded the presence or absence of the *alae* as distinguishing between *R. styliformis* Brightwell and *R. hebetata* Bailey *f. semispina* (Hensen) Gran (see p. 149). We have accepted the species as conventionally defined, and have considered the size-variations recorded within those limits.

Methods.

During routine analyses in 1938–1939 we estimated the mean size of Rhizosolenia at all positions in which it was recorded. For obvious reasons only relatively small numbers of cells (ranging from 2 to 50 according to the local density) could be measured on each 10-mile unit of the records in which Rhizosolenia was found. The major differences, however, were large enough for even a few measurements, when recorded in a large number of places, to give useful overall pictures of the spatial size-distribution. Certain of the larger patches were later selected for more detailed analysis, as also were some for each year of the 1932–1937 survey in the Southern North Sea. The samples from several of the earlier patches had been inadequately preserved for such work and useful information has often been lost, although in some cases it has been possible to obtain alternative data from the better preserved material in the "Tank Residue" (Lucas, 1940, p. 75); such data are only relevant where the record included only one well-defined patch, or when the size distribution was unimodal. In all, more than 18,000 measurements were made, of which over 11,000 were made for 1938–1939.

In various places advantage has been taken of Mr. Wimpenny's valuable arrangement whereby his detailed data are made available for other workers, some of the results of his observations being shown alongside those made in this laboratory.[1] Our method of measurement did not differ from that of Wimpenny, although the units differed. These were usually 3·7μ against his 4μ, but at times other units between 3μ and 4μ.[2] Usually 100 cells were measured on one block in the more detailed analyses, although sometimes more or less (see Appendix, Tables I and II). Despite Garstang's (1937) very justifiable plea for measurements of 200 or 300 cells in polymodal populations, it was felt that wide rather than intensive sampling should be given preference in this work. Usually, therefore, we measured only 100 cells from any one sample, although on occasions measurements of 100 and more have been made on a number of samples recorded in continuous series from one "patch." Larger samples (200–300) were taken from time to time, however, and these confirm the reliability of the smaller samples for estimating the major variations discussed below. The results illustrated in Text-figs. 2 and 6 represent an extensive selection of the material. Detailed analyses of these and all other results not shown here are available in the Department of Oceanography, University College, Hull, for consultation. Essential reference data for the selected samples (*i. e.* those samples for which size-frequency curves have been illustrated) are given in Tables I and II (pp. 168–171).

The Southern North Sea, 1932–1939.

Data for the period 1932–1938 have already been reviewed by Wimpenny (1936 and 1946). The bulk of his observations are from his "South-west Dogger Swirl Area" (practically all to the north of lat. 53° N.), and these, combined with the few results from his "East Dogger Area" almost exactly correspond in position with our data up to 1939 for the routes running from Hull to Copenhagen, Hamburg and Rotterdam, and from London to Esbjerg. Both sets of results were obtained to the south of a line from Flamborough Head to the Naze of Norway.

Wimpenny (1946, Text-fig. 2) has already shown for this area that a Rhizosolenia generation of moderate cell-size which was present in 1932 and 1933 had been completely replaced by 1934 with a second generation which first appeared as large cells in 1933, and then progressively decreased in size. In 1936 large cells appeared once more, the smaller ones gradually disappearing, and these large ones decreased in their turn throughout 1937 and 1938. Our measurements confirm these findings in general, and show that in 1939 the decrease in size had gone a stage further, whilst no further large cells had yet appeared (Text-figs. 1 and 6). There appears, in fact, to have been auxospore formation in 1932 or 1933 and 1935 or 1936. Whilst Wimpenny failed to observe auxospores in or around 1933 (Wimpenny, 1936, and Graham, 1938), he did observe them and their immediate products in 1935. We failed to observe auxospores, but recorded what appeared to be their immediate products in 1933 and 1936. It seemed likely that further auxospores might have been found in 1940 if samples could have been collected (see also p. 152).

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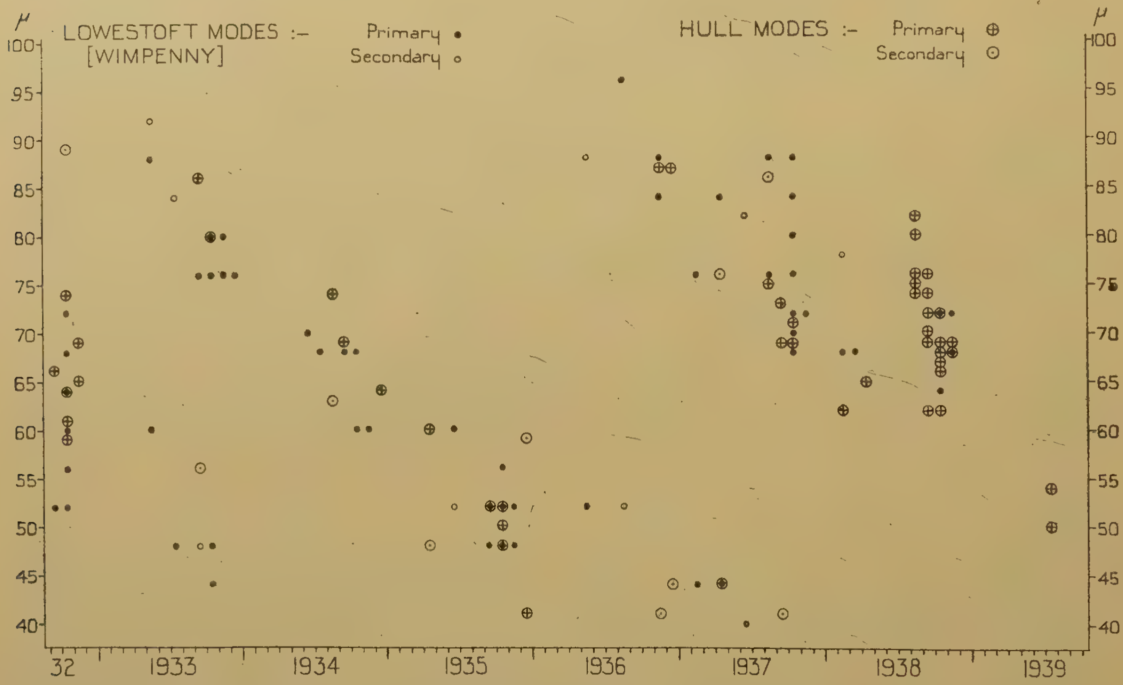
[1] We are indebted to the Marine Biological Association of the United Kingdom for permission to consult these data most conveniently.

[2] For convenience, all graphs illustrated here (including those derived from Wimpenny's data) have been plotted along the ordinate (number) as if the cells had all been measured with a constant unit of 3·7μ so that the vertical scales are comparable; points along the abscissae (size) are appropriate to the unit actually used.



TEXT-FIG. 1.—Showing month by month from September, 1932, to August, 1939, the sizes in μ of all the primary and some secondary modes of the populations of *R. styliformis* sampled with nets by Wimpenny (Lowestoft) and with the Continuous Plankton Recorder (Hull) in the North Sea to the south of a line Flamborough Head–Naze of Norway. For further explanation see text, p. 137.

In the light of earlier and rather misleading statements regarding the size-range of *R. styliformis*, it may be useful to place on record our maximum (114μ) and minimum (24μ) sizes recorded in this south-eastern area; Wimpenny's corresponding maximum and minimum were 120μ and 24μ respectively. We observed, like Wimpenny, smaller cells elsewhere (see p. 141) but none larger.

Whilst for certain purposes, and in certain conditions, it is useful to consider the means of groups of measurements, these can give misleading information regarding polymodal distributions. On the other hand, selection of a few size-frequency curves to illustrate a sequence may omit useful information, whilst it is difficult to show in one figure the whole series of curves on a linear time-scale. An attempt to overcome this is made in Text-fig. 1, where are shown the sizes at the primary modes[1] of all size-frequency curves for each month from September, 1932, to August, 1939, illustrating both Wimpenny's data and the Hull data; in addition are shown, for those months in which only one size-curve is available, the sizes at any secondary or " shoulder " modes which have been judged significant. In Text-fig. 2 (*a–h*) are shown, in relation to their positions, the size-curves of the Hull samples for the period 1932–1937, together with representative curves from Wimpenny's samples (including those to the north of the present area). Selected curves from 1938 and 1939 for this area appear in Text-fig. 6 (*a–l*), along with those for the remaining area of the North Sea.

Wimpenny's data and ours are seen to be complementary and, despite the wide modal range, the steady decrease in maximum modal size from 1933 (or possibly 1932) to early 1936 is clear, as is the sudden increase in the middle of 1936 and the second decrease to 1939. The large cells of 1936 and the first part of 1937 were accompanied by cells of a small and decreasing modal size, either at the same or at other stations, as Wimpenny has shown; some of these smaller modes were primary and others secondary. If the auxospore cycle is correctly understood, these small cells appear to be the remains of the older generation (see also p. 147). The results suggest that a similar association of old and new modes took place in 1932–1933 but, if so, the two groups of modes were then closer together in size, and the wide modal spread of the older generation in 1932 was scarcely paralleled in 1936. On the other hand, the very wide spread of the dominant modes of the larger cell-sizes in 1937 and 1938 was scarcely paralleled in 1933 and 1934. Finally, of the primary modes recorded none had a value of less than 40μ, or greater than 100μ.

The simultaneous occurrence of widely differing modes raises several points of interest. In particular, they concern Wimpenny's suggestion that size may be used as an " indication " not only of the relationships or identity of patches, but also of the life-history and the purity of any stock. It will be useful to review briefly our data for the whole North Sea in 1938 and 1939 before considering these matters. One point, however, may be illustrated here, and this is the nature of variation within an apparently individual " patch." The term " patch " has been used rather loosely to describe any concentration of plankton which tends to be isolated from others, and in its delimitation much has depended on the distances separating the samples. For Rhizosolenia, Savage and Wimpenny (1936), in accordance with Wimpenny (1936), introduced size as a means of identifying patches, and Garstang (1937) discussed by this means the probability of " mixing " within what had previously been regarded as an individual " patch " off the south-west Dogger Bank in October, 1932 (*cf.* Savage and Hardy, 1935, fig. 19; Garstang, 1937, figs. 1–3; and Lucas, 1940, Plate XXIII). We obtained one continuous record through this "patch" on the Hull-Bremen route, and found appreciable variations between the size-frequency curves for successive sections each of some two miles. Nine size-frequency curves from these successive sections are shown in Text-fig. 3. Whilst each was based only on some one-hundred measurements, so that the individual modes have not the desired signifi-

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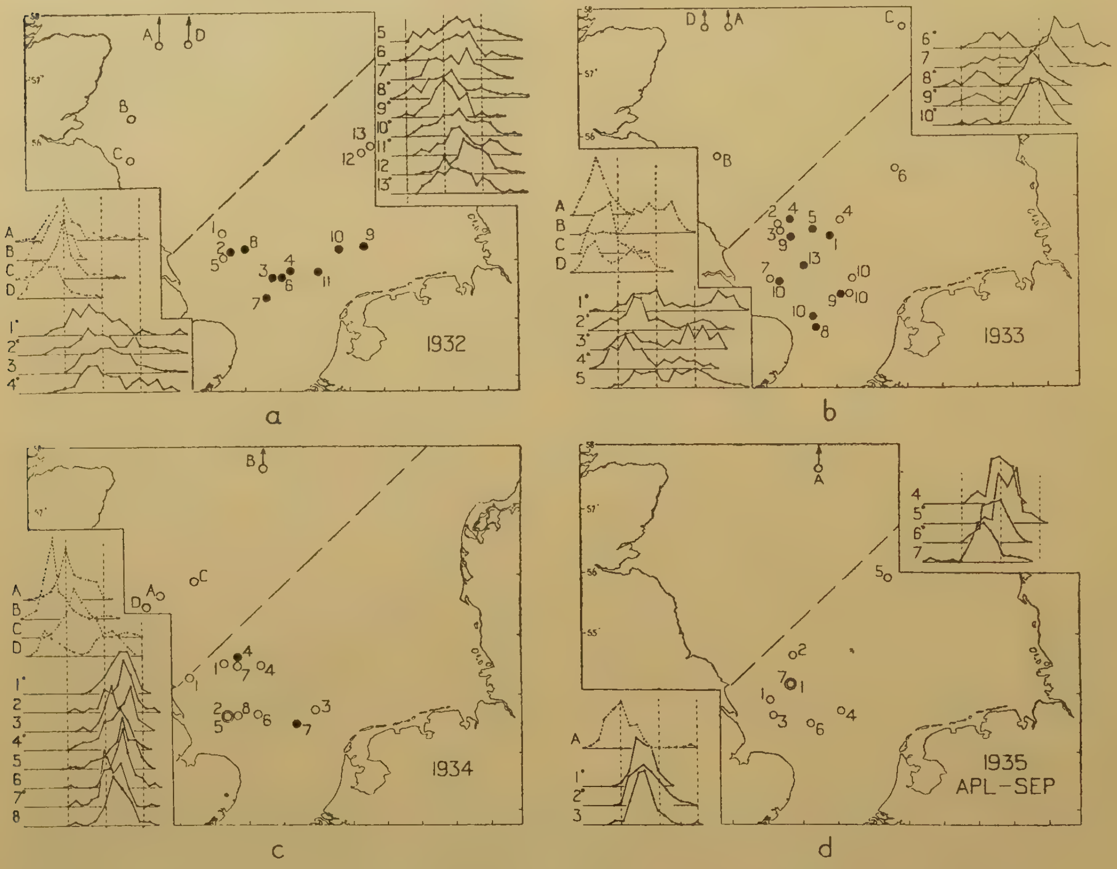
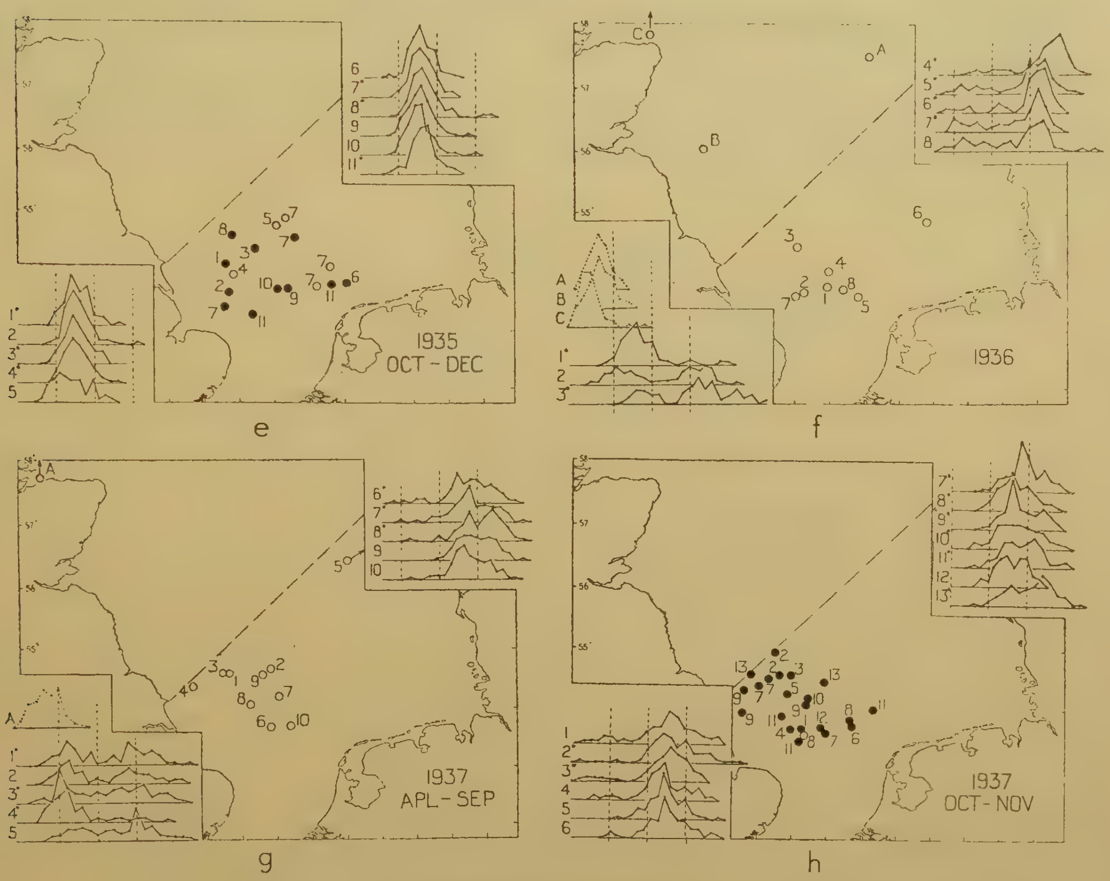
[1] The modal values have been extracted without any attempt to smooth the curves, and only one symbol has been used where two or more modes in one month coincide in size, except for distinguishing between Lowestoft and Hull samples.



Text-fig. 2.—Showing for the years 1932–1937 the positions of the samples of *R. styliformis* obtained by Wimpenny and the present writers. Those to the north-west of the line Flamborough Head–Naze of Norway are labelled by letters and those to the south-east by numbers. The blacked-in circles denote the October samples of each year, whilst the double circles indicate that two samples were obtained in the same place. [N.B.—The adjacent stations 1 and 4 in 2b have been wrongly indicated: they should be white and black respectively and not black and white.] Size-frequency curves of the different populations are shown as insets, those with the larger proportions of smaller cells being shown in general on the left of the charts and the others on the right. The size-curves of each group are labelled in date sequence and these labels correspond with the appropriate positions; where a curve has been considered as typical of more than one sample, the same number has been used for each. The broken vertical lines in each set of curves indicate the sizes of 40, 60 and 80μ respectively. All the north-western size-curves were obtained by Wimpenny; his curves for the south-eastern area are denoted by an asterisk against the reference number.

cance, the curves and the corresponding mean sizes suggest that the variations within the patch were as great as Garstang supposed, whilst there were even greater variations elsewhere in the area (fig. 2*a*).[1] In contrast is shown in Text-fig. 4 the detailed analysis of the large October patch in 1935 (Lucas, 1940, Plate XXIX). Owing to the lesser spread of sizes in this population the major modes are more significant. There was greater uniformity of size within this patch, with only slight variations from section to section, and there was fairly regular evidence of some subsidiary modes. In confirmation, Text-figs. 2*a* and 2*e* show that over all this region there was greater uniformity of size-frequency in autumn, 1935 (2*e*), than in autumn, 1932 (2*a*).



TEXT-FIG. 2.—(Continued.)

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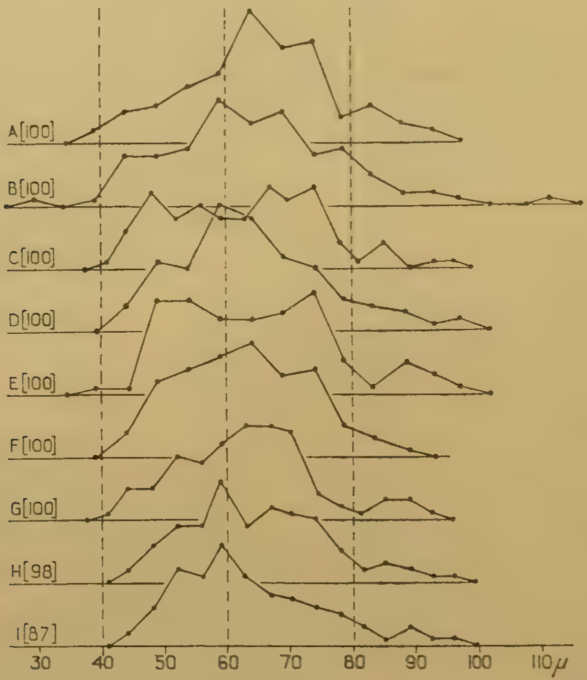
[1] The reality of significant differences within this " patch " is born out by pooling the data from adjacent sections, so that 200 or 300 cells are available instead of only 100. There still remain differences between the size-curves which would not be expected from a reasonably homogeneous patch. Two examples are seen in curves 3 and 6 in Text-fig. 2*a*, respectively from the west and east sides of the patch, which suggest a distinct increase in size moving from west to east.

The Whole North Sea, 1938–1939.

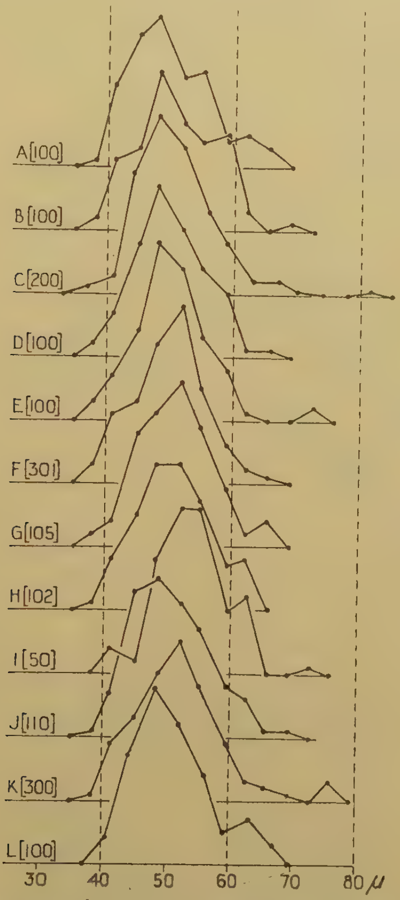
We aimed during these two years at obtaining an overall impression of the size-distribution of *R. styliformis* throughout the North Sea from estimates of mean sizes for every section of 10 miles along each route. Further information could then be obtained by measuring much larger numbers of cells on selected sections.

It has already been shown (Lucas, 1941, p. 43, and Plate VII) that cell-sizes in 1938 were appreciably smaller over the north-western half of the North Sea than over the south-eastern. This is illustrated here in Text-fig. 5 (left), showing the sizes of the *smallest* cells found throughout 1938 on each 20-mile section of record. Together with it (right) is a chart of the sizes of the *largest* cells found on each section over the whole year. The smallest cells were mainly limited to a well-defined area of the north-west, whilst the largest were mainly in the waters around the Dogger Bank. On the other hand, there was appreciable overlap among the intermediate sizes, particularly in the central North Sea. The general effect is that of two size-groups with some mixture, and it is obvious that the size-range in the south-east (some 40–100μ) is comparable with that found during 1932–1937 by Wimpenny and ourselves, whilst the north-western waters regularly



TEXT-FIG. 3.—Showing nine size-frequency curves obtained successively (each sample covering about two miles) through the chief patch of *R. styliformis* recorded in October, 1932, from west (A) to east (I). The numbers in brackets denote the numbers of cells measured. See text, p. 138.

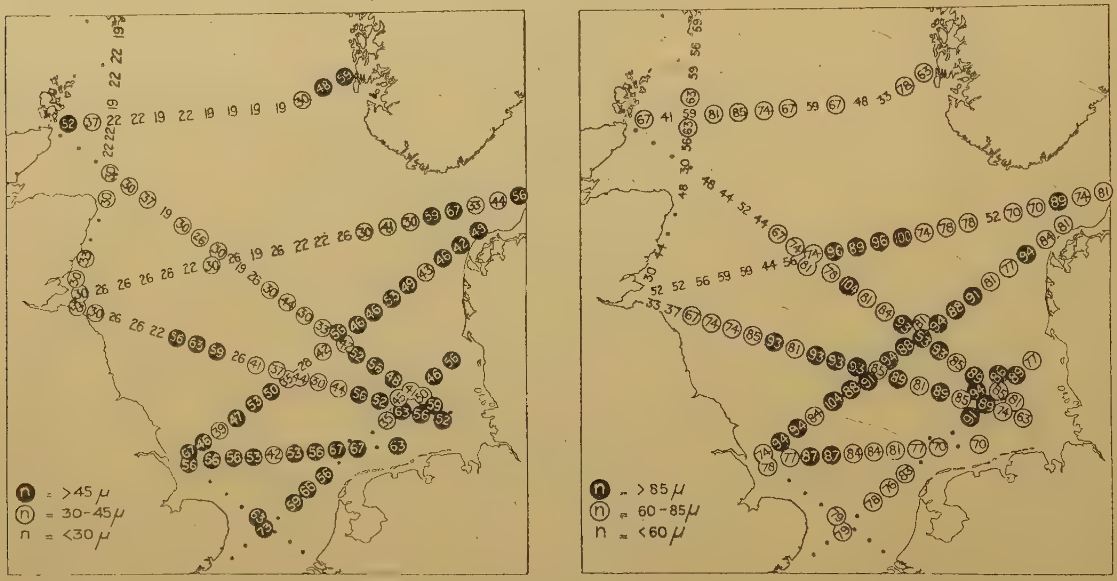
produced distinctly smaller cells (minimum = 19μ) than were ever recorded during eight years to the south of a line Flamborough-Naze. Even smaller cells were found by us on the Pentland-Iceland route in 1939 (minimum = 17μ). Wimpenny (1946) examined and measured cells from 16 stations taken in various parts of this general north-western region between 1931 and 1939 (from the Faeroe-Shetland Channel to the Firth of Forth), also finding generally smaller cells there than to the south-east (minimum = 16μ).



TEXT-FIG. 4.—Showing twelve size-frequency curves obtained successively through the chief patch of *R. styliformis* recorded in October, 1935, from west (A) to east (L). The numbers in brackets denote the numbers of cells measured. See text, p. 139.

The mean sizes of the cells on each 10-mile section are shown in detail in Text-fig. 6 (*a–l*) for successive periods from January, 1938, to August, 1939, together with representative size-frequency curves for some of our samples and some of Wimpenny's. Usually our curves are derived from a section of record not exceeding 10 miles, but occasionally all the cells obtained in two or more adjacent sections have been pooled, when the internal evidence indicated that each section had sampled a similar population. Charts showing the distribution of Rhizosolenia during this period may be seen in ‘ Bulletin ’ No. 8 (Lucas, 1941, Plates VII–XI). In general, the mean sizes may be characterized as greater or less than 50μ, and they will be referred to respectively as populations of “ large ” and “ small ” cell-size.

Records for January–March, 1938, showed “ small ” cells (modal sizes ca. 30μ) off the Firth of Forth, with “ large ” ones to the east and south. “ Small ” cells were also found to the north at that time, and were widespread there during April and May. “ Large ” cells in these two months were widely scattered in the southern waters, their north-western boundary appearing to have encroached a little on the off-Forth “ small ” area of January–March. The modal size of the “ large ” population (modes between 60μ and 80μ) apparently related directly to those of the preceding autumn (p. 136). It is noteworthy that, particularly nearer the coast, there were moderate numbers of cells around 56μ among the otherwise “ small ”-celled population off the north-east coast of Scotland.



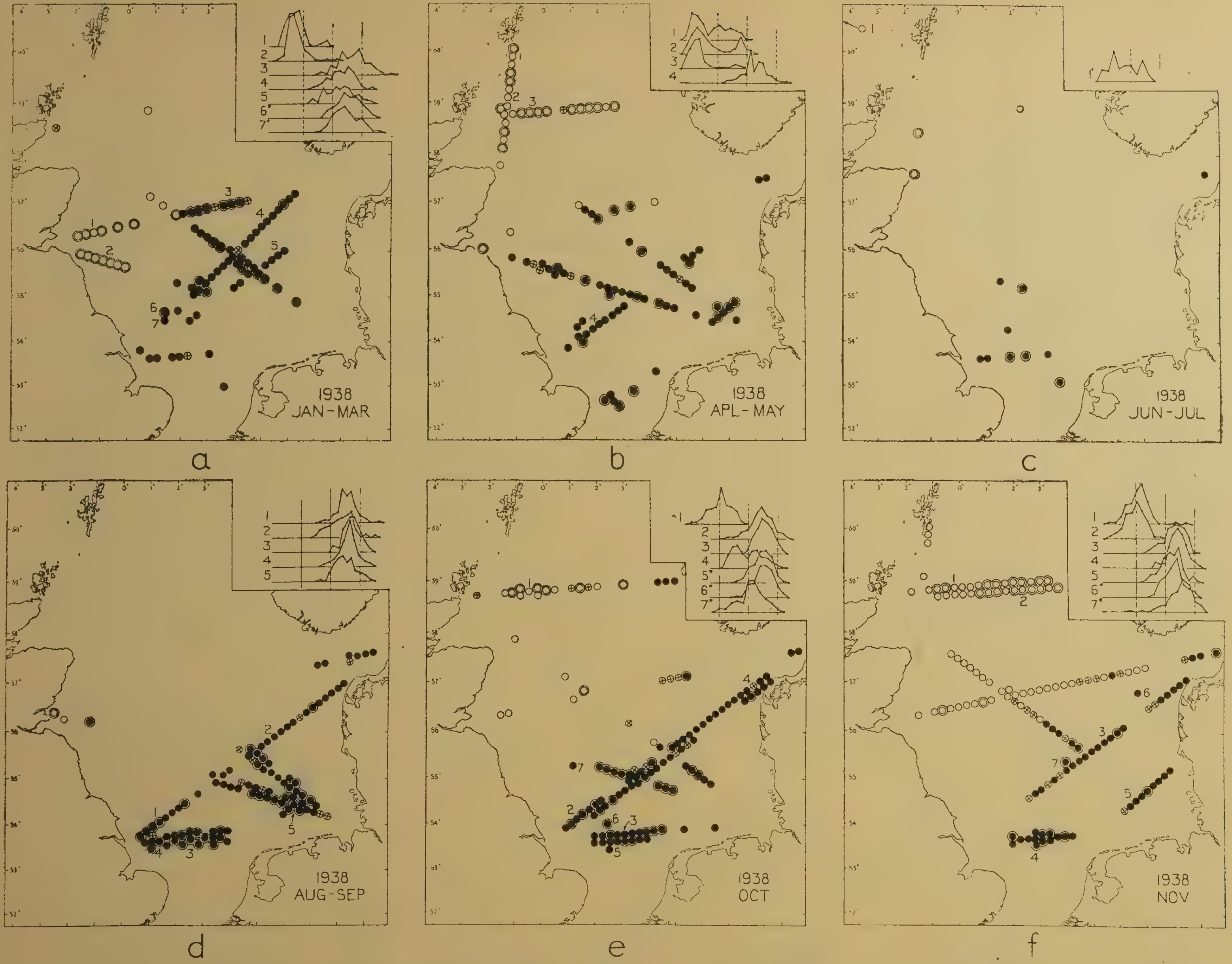
Text-fig. 5.—Showing on the left the sizes in μ of the *smallest* cells, and on the right the largest cells, of *R. styliformis* recorded on each section of 20 miles throughout 1938. Three different size-grades in each figure are distinguished by symbols (see scales).

In June and July cells were too few for useful detail, such as were measured showing no marked changes from the earlier distribution. Rhizosolenia had developed again in the south-east by August, the major size-modes for that month and September relating well to those of the earlier period. At first there were few cells below 60μ, and then more, particularly over the eastern Dogger Bank, and by October this tendency was even more marked. Meanwhile, another north-western growth had appeared (again of " small " cells), which apparently extended, although in greatly varying density, towards the edge of the central Dogger Bank in the south and towards the mouth of the Skagerrak in the east. In the north-east it gave place to a patch of cells off Bergen, the size of which suggests a close relationship with the " large " cells of the eastern Dogger Bank.

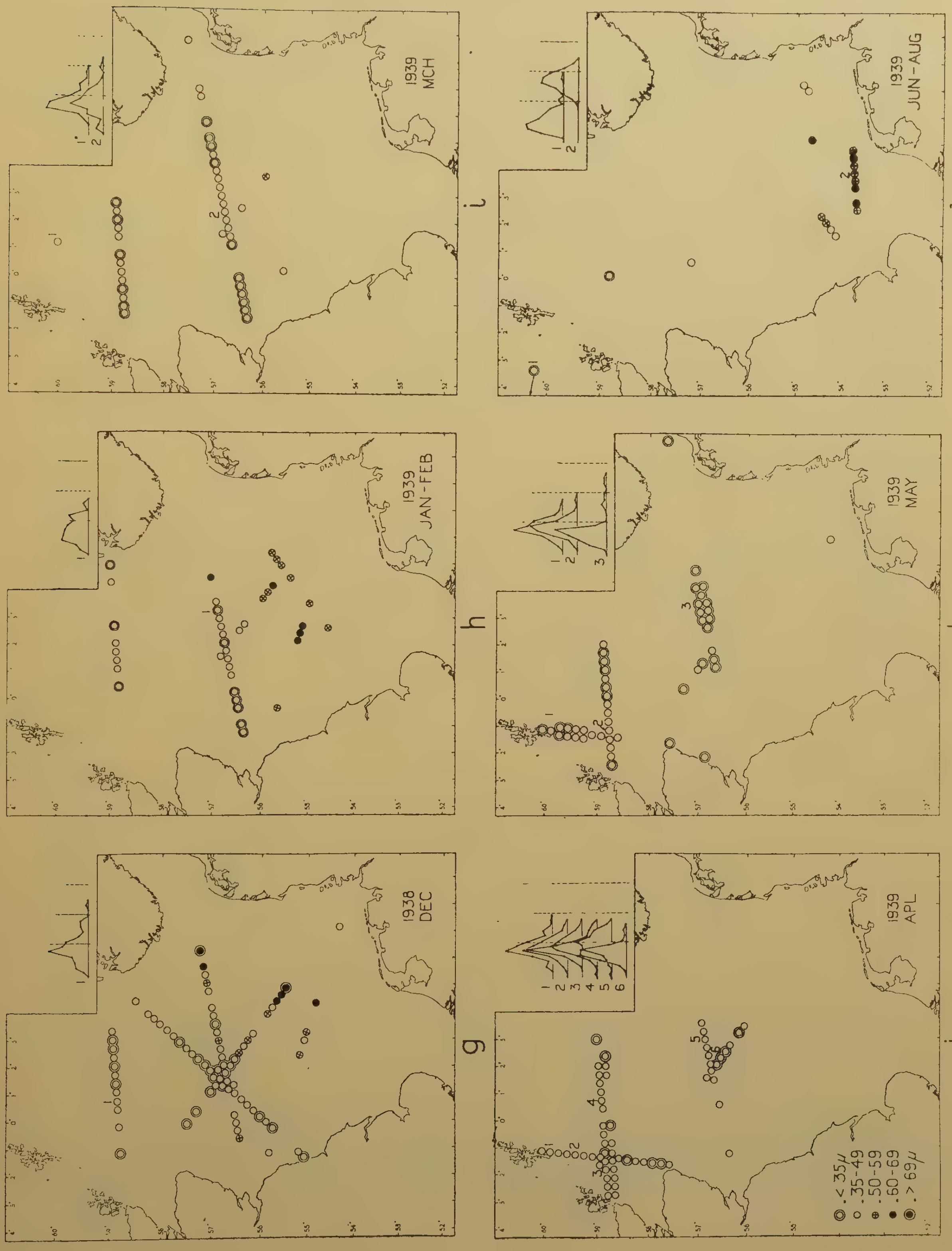
In November–December the " small " north-western cells probably covered a still wider area, extending on an irregular front up to the Skagerrak and the central Dogger region. They were by no means uniform in size, although most cells centred round 40μ ; as in the spring, a small number of relatively large cells occurred in the north-west nearer the coast. No more " large " cells were found off Bergen, and large cells appeared to be decreasing in quantity even in the south (see also Lucas, 1941, p. 29).

During this autumn period there appear signs of (*a*) the south-eastern population spreading northwards to the Norwegian coastal waters (and even towards Shetland ?), followed by its almost total disappearance, and (*b*) a spread of the north-western population towards the Dogger Bank and the Norwegian and Skagerrak waters. It is characteristic of 1938 that the " large " population probably occupied a greater area than the available records suggest for 1932–37, spreading in the spring well past the line Flamborough–Naze towards the Firth of Forth. Such distributions show that the additional information available from size measurements adds considerably to that available merely from records of population density (Lucas, 1941, Plates VIII and IX). Whilst mixing between the large and small populations occurred, examples of the abrupt nature of their boundaries at times may be seen in Text-fig. 6 (charts *a*, *b*, *e*, *f* and *g* for 1938 and *h* for 1939). Seldom is there sufficient data available to supply detailed studies of the size changes on a series of successive sections, except well within the productive centres of the two regions (*cf.* Text-figs. 3 and 4). Particular examples of the abrupt boundary changes are seen on the Leith–Copenhagen line for January, October and December and the Pentland–Hamburg line for October, November and December, but it is characteristic of the boundary regions that they are also regions of low numbers or absence in our records (*cf.* Plates VIII to XI in ' Bulletin ' No. 8), so that size data are scarce or often absent where they are required for this problem. This last point itself is suggestive of a boundary between two usually distinct groups, and so is the general scarcity of size-curves with " intermediate " modes, as opposed to the usual recording of curves with modes characterizing one or the other, or even both, populations.

From December, 1938, to July, 1939, " large " Rhizosolenia were very scarce, as, in fact, were any cells in the south-east. " Small " cells populated the northern waters, their dominant modes decreasing generally towards 30–35μ, as we found in the spring of 1938. Not until July did Rhizosolenia become even moderately abundant in the south, when patches developed in the now familiar position near the South-west patch of the Dogger Bank. The modal size then, 53μ, was appre-


a
1938
JAN-MAR
b
1938
APL-MAY
c
1938
JUN-JUL
d
1938
AUG-SEP
e
1938
OCT
f
1938
NOV

TEXT-FIG. 6.—Showing the mean sizes in μ (see scale inset in Chart j.) of *R. styliformis* in the North Sea for each recorded section of 10 miles during twelve consecutive periods from January, 1938, to August, 1939, together with those of nine samples obtained by Wimpenny (see text). Selected size-frequency curves of the different populations are shown as insets, the curves being labelled with numbers to correspond with their positions. Wimpenny's curves are denoted by an asterisk against the reference number. The broken vertical lines in each set indicate the sizes of 40, 60 and 80μ respectively.


g
1938 DEC
h
1939 JAN-FEB
i
1939 MCH
j
1939 APL
k
1939 MAY
l
1939 JUN-AUG
1
2
3
4
5
6
◎ < 35μ
○ .35-49
⊕ .50-59
● .60-69
◉ > 69μ

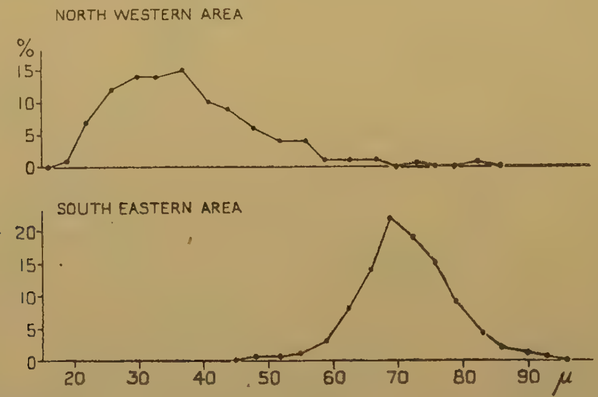
TEXT-FIG. 6.—(Continued.)

ciably smaller than those typical of the previous autumn (particularly in this position), despite the apparently poor growth of the previous eight months. In July, too, we were able for the first time to record the size distribution between Pentland and Faeroe, where a smaller size-mode (23μ, minimum size = 17μ) was recorded than any found elsewhere by us; this was accompanied by a distinct "shoulder" at 35μ, roughly corresponding with the size recorded as the major mode in the north-western North Sea in May.

Wimpenny (1946) obtained less information for 1938 than in the earlier years (*cf.* his Table I) and only one northern observation in 1939. Some of his size-frequency curves are shown in Text-fig. 6, and there appear to be no obvious discrepancies between the two sets of size data where comparable. In fact, our data confirm fully his view that cells "were much narrower in the northern North Sea and Faeroe-Shetland area" than in the Southern North Sea. It is less certain that the Firth of Forth Swirl Area presents "an intermediate stage" (his p. 12), except in space, since the cells may be smaller or larger than some found to the north.

The Stocks of R. styliformis.

The fairly detailed results for the twenty months of 1938–1939 over a wide area immediately prompt the following questions: (1) How far were these years "typical" and, if they were typical, can we then normally distinguish by size at least two populations of *R. styliformis* in the North Sea?: (2) How far do they mix, and with what results?; and (3) What are the relationships of these populations to other Rhizosolenia populations? Related questions concern Wimpenny's discussion (1946) of the varieties of *R. styliformis.*



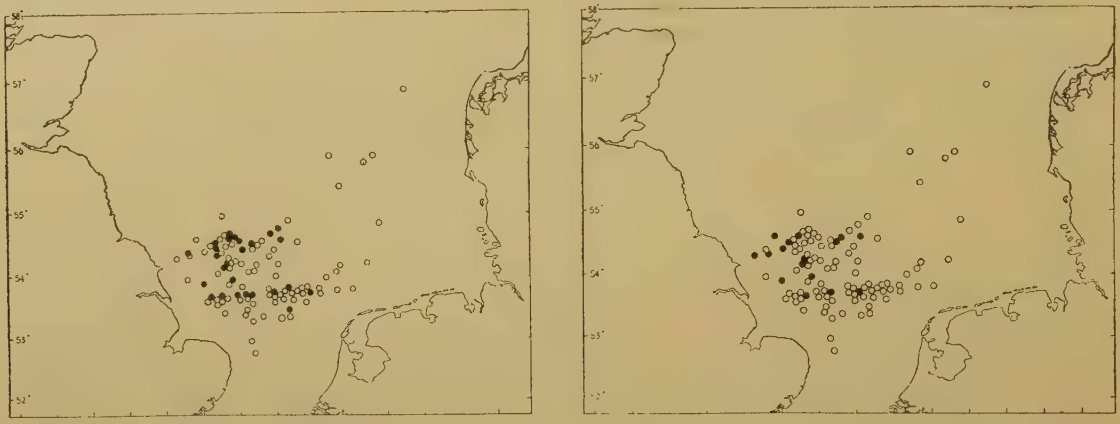
TEXT-FIG. 7.—Showing the percentage size-frequency in μ of 1345 cells of *R. styliformis* obtained during 1938 in the north-western area and 1816 cells obtained in the south-eastern area.

During both 1938 and 1939 there undoubtedly appear to have been at least two size-groups, north-western and south-eastern, with varying mixture along their boundaries; in addition, each of these presented local size-differences, Whilst there was mixing between the two main size-groups at times, in general their more typical size-frequency curves showed little or no overlap during these years. This is further illustrated in Text-fig. 7, presenting size-curves for 1345 cells from the north-west and 1816 from the south-east, each based on the summation of many samples taken well within their respective areas throughout 1938. " Small " cells were less frequently found in the south-eastern samples than were " large " ones in the north-western ones.

We have by no means suitable material for deciding how far these years were typical, except in so far as the whole of Wimpenny's data and ours point to the existence in the south-eastern area for the six earlier years, 1932–1937, of a stock of *Rhizosolenia* to which the south-eastern stock of 1938–1939 bears a logical relationship in size (Text-fig. 1). Wimpenny's north-western data, too, accord well in that, from 1931 to 1939, there were on each available occasion principally " small " cells (modes ranging from 29–48μ) in his Shetland area, although not without admixture of some larger cells, as we also found. Six out of seven of his Firth of Forth Swirl samples are similar (modes at 28–44μ, although one of these was accompanied by an equally strong mode at 64μ, and another had a major mode at 68μ associated with much smaller cells). His two samples collected off the southern coast of Norway were also " small " (as were his six samples from south-west of the British Isles in 1939). In every instance the mean sizes of these samples were lower, usually much lower, than those obtained at a corresponding date in the south-eastern area of the North Sea. On this evidence alone one might reasonably decide that the 1938–1939 data were not markedly abnormal, and that from 1932 to 1939 there had usually been at least two populations which were broadly distinguishable by size.

In addition to showing the positions of the various samples obtained during 1932–1937, Text-fig. 2 also shows representative size-frequency curves. All those for the stations to the north of the line Flamborough Head–Naze of Norway (Wimpenny's samples:—stations and curves denoted by letters) are shown on the left of the charts, in broken line. Representative curves for the much more numerous south-eastern stations (Wimpenny's samples and Hull samples combined, and denoted by numbers) have been selected to illustrate the major size-differences, and are shown in continuous line. These have further been divided into two groups according to the proportions of smaller cells in the samples, those with the greater proportions of smaller cells being shown on the left and the others on the right of the charts (except in 1934, when the differences were very slight). Within each group the curves are arranged in date order and numbered consecutively; where any curve has been considered as representative of more than one position, the same number has been used for each of those positions.

When viewed in this way, it is seen that, in general, those samples having the greater proportions of smaller cells were relatively commoner in the west or north-western part of this S.E. area. This is shown by both Wimpenny's data and ours (*cf.* Wimpenny, 1936, p. 40, and 1946, p. 281), and can be seen in 1932, 1933, 1936 and 1937, and the early part of 1935. In 1934 and part of 1935 the differences were very slight, although, even in the latter part of 1935, the size-differences showed the smaller cells to be rather commoner in the west. This spatial difference is revealed in Text-fig. 8, where on the left are distinguished from the rest the positions of those samples having the greatest proportions of smaller cells in each of the charts of Text-fig. 2, three from each chart; whilst on the right are distinguished all those samples seen in Text-fig. 1 to have a size-mode at less than 50μ. The two criteria here adopted are by no means the same, and so the stations are not identical, but both methods agree in showing that smaller cells tended generally to be grouped around the South-west Dogger Bank, whilst they were absent in the north-eastern part of the area. If we consider the stations lying to the north of Lat. 54° N. and west of Long. 3° E., then out of these 38 stations 13 in the left-hand chart and 10 in the right-hand chart ranked as "smaller," whilst correspondingly only 13 and 5 were so ranked out of the remaining 65 stations to the south and east. An additional complication may be that it is not entirely possible to separate such a spatial segregation from a temporal one, since rather more than half of the "smaller" south-eastern samples were obtained in months before September, although less than one-quarter of all samples were obtained before that month.

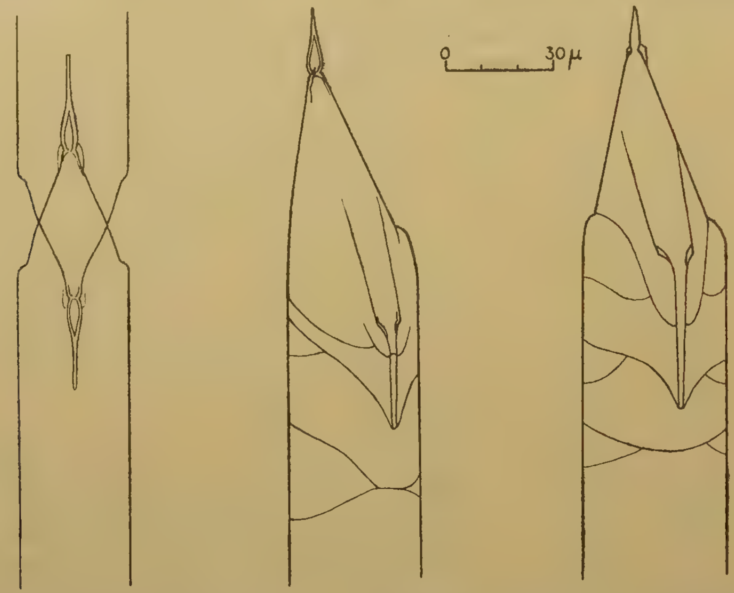


Text-fig. 8.—Showing on the left the positions of the three "smallest" south-eastern samples (●) of *R. styliformis* derived from each of the charts of Text-fig. 2, together with the positions of all other south-eastern samples obtained during 1932–1937. On the right are shown the positions of the same samples, but distinguishing (●) all those having a mode of less than 50μ in Text-fig. 1 (see text, above).

Two possible explanations for this spatial arrangement are: (1) that the larger proportions of smaller cells are the result of invasions from the neighbouring waters to the north-west, which we know to have been usually populated with small cells; and (2) that, as is suggested by the data obtained from Text-fig. 1, the smaller cells naturally occurring towards the end of an auxospore generation tend to be more frequent over the South-west Dogger region. Regarding the first possibility, we must emphasize that in most cases the dominant size-modes to the north-west (*e. g.*, off the Forth) were distinctly smaller than any even of the secondary modes of the south-eastern area; although two north-western samples in 1933 showed size-modes (one of them dominant) which were not very dissimilar from the south-eastern ones, as did at least one in 1934. In so far as these last suggest invasion or mixing, it might appear that they arose more from north-going movements than the reverse. Whilst there is every reason to suppose that southerly invasions occur (see p. 143), it does not appear likely that they were responsible for such high proportions of small cells as occurred over the South-west Dogger by the actual carriage of such small cells, and this brings us to the second suggestion once more, with which may be associated Wimpenny's (1946) reference to the "revival" of the old generation in 1937 (his fig. 2), in possible relation to salinity changes. (There may have been a somewhat similar occurrence in 1933.) There can, in fact, be little doubt that, in this spatial differentiation, we are principally concerned with an unusual abundance of cells of an old generation within a limited area and/or time. Simple mixing may also have occurred in this region, or to the north and east (as in 1938), even though not readily detectable, and we must remember the regular occurrence in these same waters of the South-west Patch of an animal community resembling more that of the north-western than the rest of the south-eastern region (see, *e.g.*, Russell, 1939; Rae and Rees, 1947; and Marshall, 1948).

At this stage it seems suitable to discuss briefly the nature of the two size stocks we have reviewed. Following his examination of the structure of *R. styliformis* from various localities, Wimpenny (1946) suggested a subdivision of the species into the type and two varieties, of which his type was potentially large and was considered characteristic of the Southern North Sea. Nowhere in our "south-eastern" region did he record any other than the type, although he found it elsewhere in British waters from off Shetland to the English Channel (where it was the only form named by him). In his northern samples he also distinguished two varieties: var. *semispina*, essentially having obtuse-angled wings extending along the apical spine, and with a tongue in the first intercalary plate; and var. *oceanica*, essentially distinguished by its rounded wings. With one exception from antarctic waters, all his measurements of these two varieties showed them to be small, as were his *typica* cells from Scotland and the English Channel. All but one of his Forth samples were judged to be *typica*, and they were usually small, as we have seen.

It has not been possible to re-examine the Hull material in the light of Wimpenny's suggestions, but it should be stated that in the limit, like him, we met some difficulty in separating the smallest *R. styliformis* Brightwell from *R. hebetata semispina* Hensen. The criterion of the presence or absence of the *alae* was adopted, and to this extent we believe that the generally adopted specific boundaries were maintained. We are inclined, however, to agree with Wimpenny that there may arise reasons for considering whether these two species are not more closely related. Whilst we saw cells corresponding to his var. *oceanica*, they were relatively rare in our records, and were at the time regarded, like other exceptions we saw, as abnormal specimens. In the light of Wimpenny's detailed observations it now seems probable that they have greater significance, and we take this opportunity to illustrate in Text-fig. 9 the main features of other, "shouldered," forms we have seen in northern waters. It seems possible that *R. styliformis* may prove to be part of a polyphasic system (Hendey, 1937). Wimpenny considers that both in the northern area and in the English Channel Rhizosolenia has a much shorter auxospore cycle than in the Southern North Sea, but we have no certain evidence with which to test this suggestion. The problems and suggestions raised by Wimpenny are most important, and it is hoped that they may be resolved in time by as detailed work outside the Southern North Sea as that which has so far only been possible within it.



TEXT-FIG. 9.—Showing the outline structure of "shouldered" forms of *R. styliformis* at times recorded in the northern North Sea during 1938–1939 (see above). We are indebted to Mr. R. S. Glover who provided the drawing for this figure.

However this may be, evidence for at least two major size-divisions of *R. styliformis* seems to be well established, of which the smaller must include Wimpenny's two varieties. As Wimpenny has suggested, one obvious environmental difference between their regions is that of salinity. In general the smaller north-western cells must have been found in water of higher salinity than that of their south-eastern neighbours, and the smallest group we found (Faeroe-Shetland) is likely to have been associated with the highest salinity of all. Yet, whilst these groups are associated in general with waters of different salinity, it still seems unlikely that they exist as simple reflections of this environmental factor. If this were so, we should have expected far more size-frequency curves having " intermediate " modes (as distinct from characterizing chiefly one or the other population, or occasionally both), and it must seem likely that there are other factors concerned. However, in the light of the evidence to be reviewed regarding the probable effects of salinity on the sizes of *Biddulphia sinensis* (p. 160), it is certainly tempting to associate the periodical finding of higher proportions of smaller cells over the western Dogger Bank than elsewhere in the Southern North Sea, with the tendency for the waters of the South-West Dogger Bank Swirl to be of relatively higher salinity. With such a suggestion, we can at once include (1) the possibility of small north-western cells directly invading the southern waters, and (2) a possible favouring by higher salinity of the smaller cells among all those giving rise to the Rhizosolenia flowering each year around the Dogger Bank, and particularly its South-west Patch. For example, on occasions, the old generation might be favoured (particularly with abundant nutrients) at the expense of the contemporary new one as Wimpenny suggested. Local auxospore generation might even be delayed. On the other hand, any northerly translation of less salt water towards the Forth might not only cause mixture of the two populations, but might also affect the size of the local north-western one. Such northern translation may have occurred in 1933 and 1934, and in the spring of 1938 (p. 142), but in 1932 and 1936, and from the autumn of 1938 until the end of the survey, the stock off the Forth appears to have been fairly pure. There is no suitable data for 1935 and 1937.

Whilst separating his " type " cells from his var. *semispina*, it appears that Wimpenny looks on the " type " cells as essentially a single form but showing in space certain physiological differences (size and auxospore cycle). Without any discussion of varieties, Garstang, in contrast, referred to the existence of coastal, Dogger and Forth stocks, with mixture of the first two, and the possible derivation of the last from the second. For Wimpenny, the north-western Rhizosolenias are in part small " type " cells mixed with " semispina " and in part " oceanica " cells. That the cells of the south-eastern population move away to the north-east is very probable, as may be seen in the detailed records for 1932–1939 (Lucas, 1940 and 1941). In 1938 the present survey traces the large cells as far north as Bergen in October, and it is possible that some of the larger cells found among the north-western population were carried along with *B. sinensis*, etc. (Lucas, 1941), in the great northern eddy (Tait, 1937, fig. 48). Further than this we cannot yet say. It may have happened in other years, but as yet we have no indications of any appreciable growth of large cells in the north-western waters. Whether, if there is invasion of the large " south-eastern " cells, they change their size in response to higher salinities (or only find a suitable habitat in local, perhaps coastal, water of lower salinity), or whether they are greatly outnumbered by the growth of the small north-western cells within their own habitat, is uncertain. What does seem certain is the relatively clear-cut boundary between two populations, a boundary which, despite the evidence of mixing, is sometimes abrupt enough to suggest that factors other than those merely of salinity may be concerned (p. 143 and Text-fig. 6). Our present knowledge of salinity changes in this region does not reveal such abruptness, although later work may yet show it. The evidence points rather to at least two quite different stocks, either of which may itself be affected by salinity, but which normally are identifiable by distinct size differences even at times when the " large " south-eastern cells are in the " old " and small stage of their cycle. Such a formulation of the results does not preclude a subdivision of either of these two into further identifiable populations. In the south, for instance, there are at times (*e. g.* 1937 and 1938) signs of more than one size group even among the large cells of a fairly new generation. In the north, again, there are modal differences which as yet cannot be interpreted simply in terms of auxospore generations. On the whole, Wimpenny's results appear in sympathy with these suggestions, although we are not yet able to discuss our results in terms of his varieties. The relations between the two size-groups are such that, for example, the area of the north-western one may broadly be compared with the *Sagitta elegans* area of Russell (1939, fig. 5), and with that of the zooplankton indicators of north-western water enumerated by Rae and Rees (1947) and Marshall (1948). The south-eastern stock is, of course, that illustrated by Russell, in his fig. 5; it generally occupies an area inhabited by *Sagitta setosa* and closely resembles that of the copepods Labidocera and Isias, as shown by Rae and Rees (1947, Text-figs. 6 and 7).

The known interrelations between the two stocks are just what one might expect from the inhabitants of such water masses. They occupied similar areas to those of the other organisms and, whilst their boundaries were similarly abrupt at times, they mixed at other times in a similar way. In particular, we have shown on pp. 142–5 the varying interrelationships of the two diatom populations during the autumn of 1938. It can now be seen that the spread of the " small " cells then agreed reasonably with our detailed information of the spread of Clione and *S. elegans* southwards and eastwards (Marshall, 1948), as also that of various copepods (Rae and Rees, 1947). There were related movements of diatoms (Lucas, 1941) and young fish (Stubbings and Henderson, in press). Again, the appearance of " large " cells near Bergen in October parallels the finding of *S. setosa* there in December, and perhaps Clione in September. It becomes tempting to regard the sizes (or varieties) of Rhizosolenia as " indicators " resembling certain zoo-plankton species. Regarding the more formal and systematic relations between the size-groups of Rhizosolenia, and within the north-western stock as here considered, more detailed investigations will be made, if possible, during the present survey.[1]

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[1] Preliminary examination of the scanty material collected in 1946 shows in general a similar grouping of larger and smaller cells to that seen in 1932–1939. In particular, the sizes of the larger ones—some 50–60μ—is roughly what might have been anticipated for the south-eastern area in 1946, assuming the size-cycles observed in 1932–1939 to have continued similarly during the war years. We may thus imagine peak sizes to have occurred in 1940 and 1944, the data for 1946 corresponding in size with that of 1935, 1939 (and 1943 ?).

One remaining point may be dealt with here, concerning the rates of change in cell-size in the south-eastern stock. There is general evidence that size decrease occurs in relation to cell-division following auxospore-formation, suggesting that the rate of decrease might be a measure of the number of cell-divisions—theoretically one of the few ways in which the total production of any one species might be estimated. However, we do not know the conditions governing auxospore or other spore formation, and it seems most likely that salinity changes at least can influence cell-size in a patch (see p. 160). Either or both of these processes may have contributed to the distinctly bimodal nature of the size-frequency curves of the larger cells in 1933–1934 and 1936–1938, and perhaps in 1932. It is, in fact, a matter for surprise that the size-cycle should be as recognizable as it is, for we should also allow, within the area of any one stock, for the very varied rates of multiplication within and without the various "patches." One might have visualized one lot of cells dividing so much faster than another that as a result auxospore formation might occur at widely different times, and that after a relatively short time no widespread cycle should be recognized. We are forced to conclude that either (1) the formation of auxospores (or other spores) is governed more by an external than an internal factor, or else (2) the rate of multiplication of the most favoured cells is such that in any season their products become so much more numerous than all others as effectively to govern the size-cycles; that, whilst there are many spore-formations and cycles, only one (or perhaps two rather close in time, as some of the evidence suggests) is effective, and so identifiable, by sheer weight of numbers. There may be some support for this in the regular recording of only a few, sometimes only two or three, major "patches."

Biddulphia sinensis GREVILLE.

Methods.

When arrangements were made to measure *Rhizosolenia styliformis* it was felt desirable also to obtain measurements of other forms of phytoplankton, particularly *Biddulphia sinensis* and some of the Ceratium spp. This was impossible at the time, and we have not yet been able to make any detailed measurements of Ceratia, but we were later able to do so for *B. sinensis*. Since this delay meant returning to old material, for several reasons we were not often able to make measurements on every available section of a record; although this was done in some cases, we usually selected particular samples, in relation to some recorded "patch," for analysis. These samples were also selected, in part, in relation to size-differences which were known or anticipated.

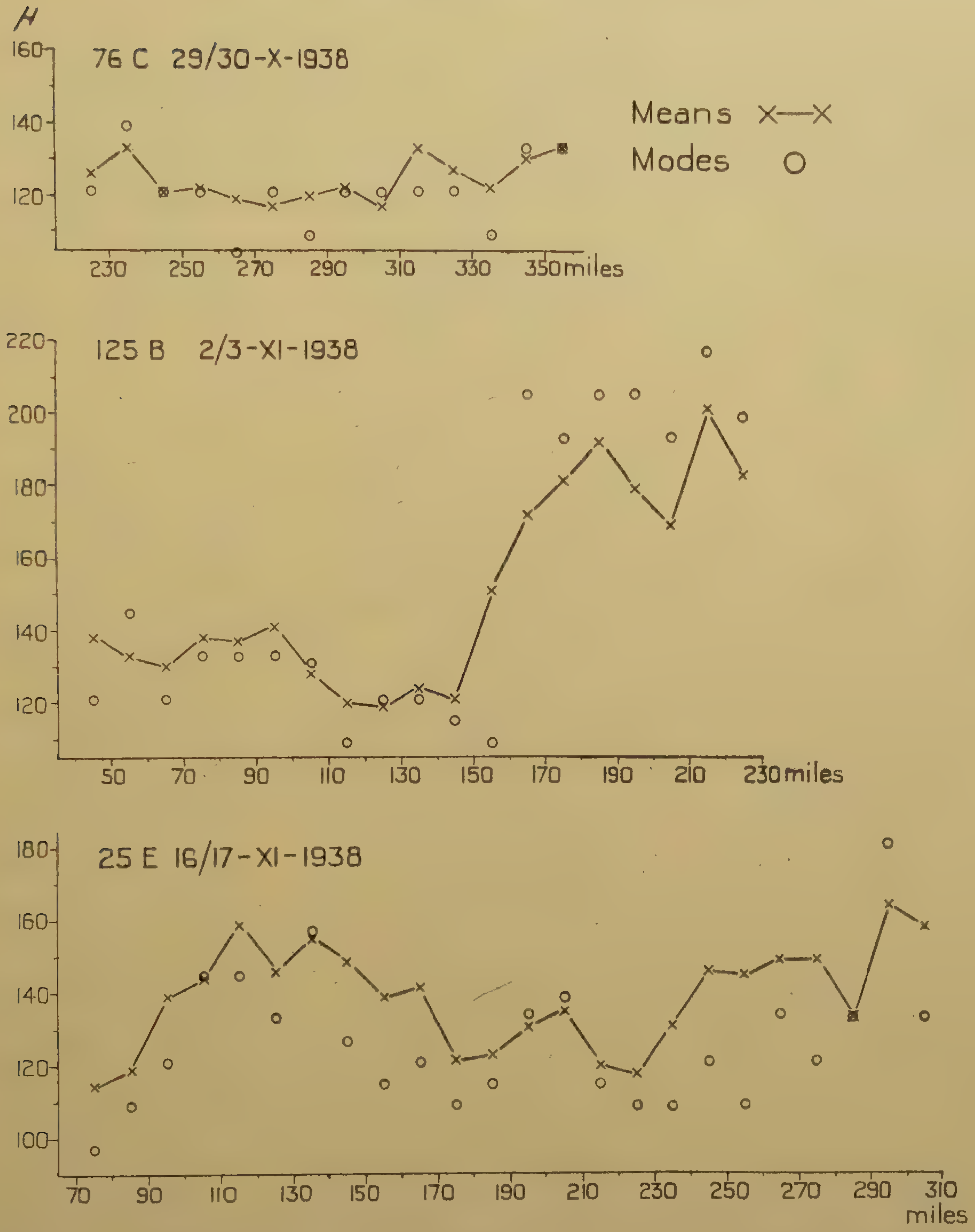
In all, nearly 20,000 cells have been measured, of which more than 13,000 were measured in 1938. Two units of measurement have been used, 12·1μ for the majority, and 15·3μ for the remainder. As with *R. styliformis*, it may be useful to record the maximum (278μ) and the minimum (46μ) sizes noted over the nine years 1931–1939 (there was only one sample available in 1931). This range is much greater than that usually recorded, and it is likely that similarly wider ranges would be recorded for most other phytoplanktonts under detailed measurement. Wherever possible, at least 100 cells were measured and often more. Occasionally only 25 or 50 could be obtained.

Sizes.

In order to indicate the general nature of the Biddulphia findings, Text-fig. 10 has been prepared to show the mean and modal sizes of all cells measured on successive 10-mile sections of three records taken during October and November, 1938. These records sampled the patches illustrated in ' Bulletin ' No. 8 (Lucas, 1941, Plate XIII). The results for 140 consecutive miles of the Hull–Copenhagen route (76C) show a fairly small variation, although it appears that there was a significant decrease in size, followed by an increase, moving from west to east. Turning now to the Hull–Hamburg route (125B) there was a comparable decrease, moving from west to east, followed by a very large and consistent increase. A significant change appeared to occur between the 10-mile sections 15 (140–150 miles) and 16 (150–160 miles). The data for the London–Esbjerg route (25 E) crossing section 15 of the last route with its section 17 (160–170 miles) showed a steady increase from a small group of means to moderately large, then to irregularly smaller ones again, followed by moderately and then quite large ones.

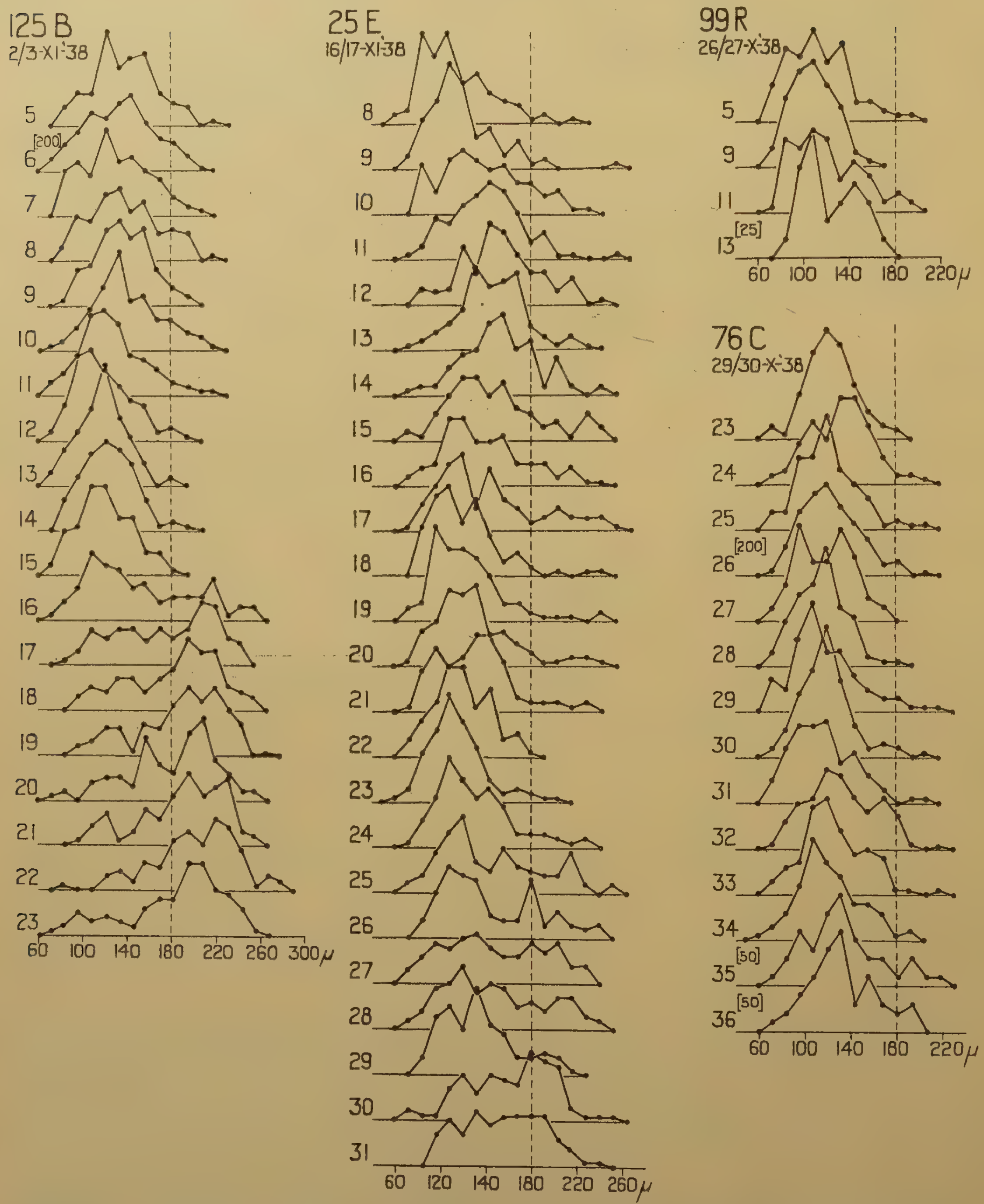
Text-fig. 11 shows that there is no reason to doubt the significance of the major variations of the means. In this figure the numbers 5, 6, 7, etc., one against each curve, denote the 10-mile sections and correspond to the mile scale in Text-fig. 10 (40–50, 50–60, 60–70 miles, etc.). The size-frequency curves from each section are presented for these three records and also for the Hull–Rotterdam record (99 R) of similar date. Whilst there is some modal variation on route C, all modes lie between 97 and 145μ and most between 109 and 133μ. Most curves are skewed to some extent, and the chief variations in mean size lie in variations in the degree of skewness. The B record presents additional evidence and, even over the western part of the record, changes in mean appear to have reflected small changes in mode. Between sections 15 and 16, although a small mode remained dominant, a much larger one (of which there had at most only been a trace earlier) was secondary to it. This had become dominant by section 17, and remained so with small variations until the eastern end of the record was reached. The smaller mode, however, remained as an appreciable characteristic of the population, and cells were found at the eastern end as small as any elsewhere. Means on this record reflected real modal changes, and were not very far removed from the modal values.

The results from the E record carry us a step further. In general, the means reflected the modes, and were usually higher than them (reflecting skewness), but in some places the primary modes shot well above the mean, as in the eastern part of the B route. In general, skewness was most pronounced in this route, and the size-range with one exception (section 22) is large. Unlike the comparative



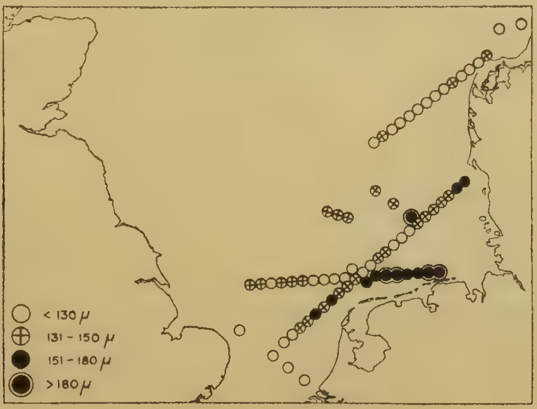
Text-fig. 10.—Showing the mean and modal sizes in μ of samples of *B. sinensis* measured on successive 10-mile sections from west to east of the routes from Hull to Copenhagen (76C) and Bremen (125B), and from London to Esbjerg (25E). For positions see Text-fig. 12.

uniformity of the modes on the C and B records, the modes on E were constantly shifting, usually by gradual changes. The four curves obtained from isolated sections of the R record had a constant major mode, although the eastern samples each had a larger shoulder in addition.



TEXT-FIG. 11.—Showing for each of the samples of Text-fig. 10 the size-frequency curves of *B. sinensis*, together with those from four 10-mile sections of the Hull–Rotterdam route. The sections are numbered from west to east (for positions see Text-fig. 12). The measured samples were all of 100 cells except where indicated otherwise, thus 6[200], 26[200].

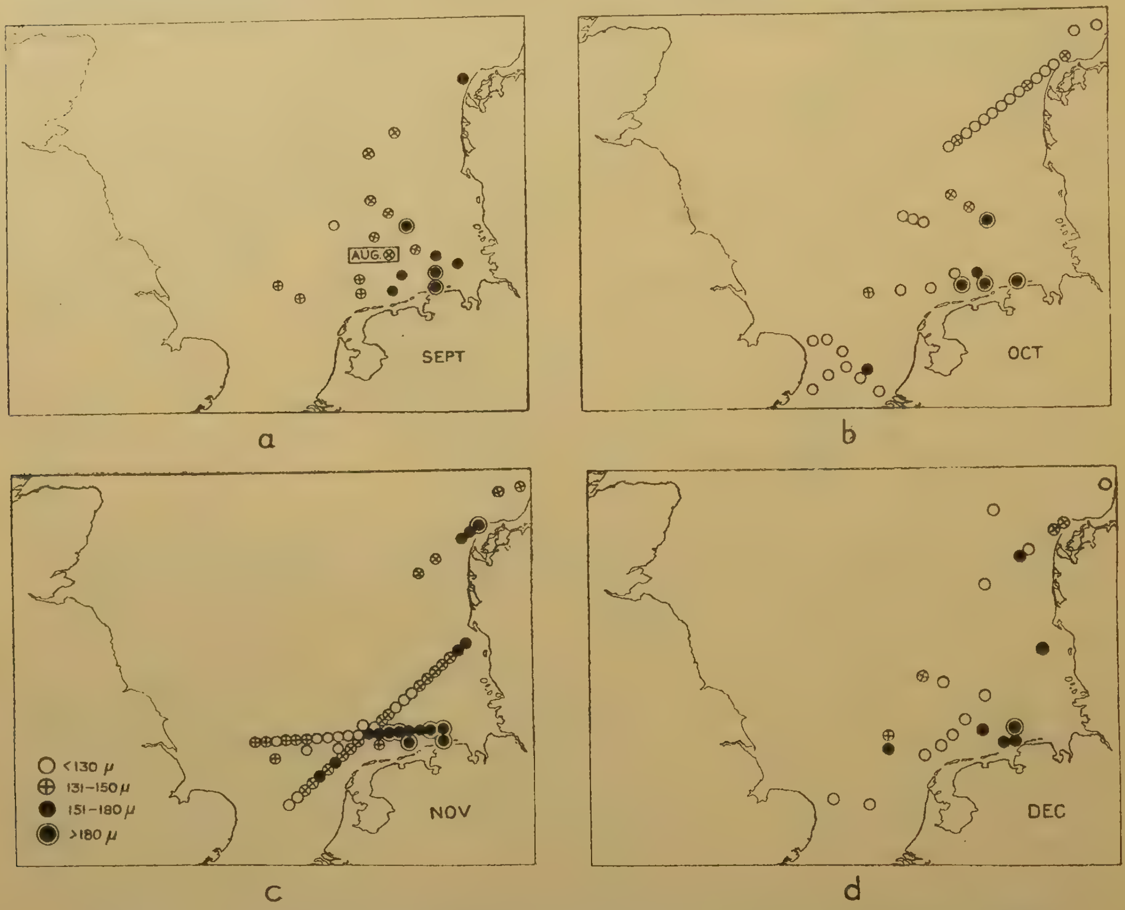
In general, it may be said that the mean size has provided useful information about changes at this time. Despite the known dangers of its use (it could, for instance, fail to represent the size of any cells measured in the case of extreme bimodality), it revealed the major changes to be seen on these occasions. Whilst looking for instances in which it will be misleading, it will now be used as a first guide to the major spatial and temporal changes in size of *Biddulphia sinensis* from 1931 to 1939.



Text-fig. 12.—Showing the positions and mean sizes of the samples of *B. sinensis* illustrated in Text-figs. 10 and 11 (i.e., recorded on routes between Hull and Copenhagen, Bremen and Rotterdam, and between London and Esbjerg), together with a few others obtained during the period October 11th to November 16th, 1938.

In Text-fig. 12 the results discussed above have been charted together with such other records as occurred within the same 37 days (October 11th–November 16th, 1938); most of the results (those discussed above) occurred within 21 days (October 26th–November 16th). In conjunction with Text-figs. 10 and 11, we can distinguish a zone near the continental coast in which " large " cells were abundant or predominated (means $> 150\mu$). Among the remaining observations can be distinguished a region of " small " cells ($< 130\mu$) in the south, extending across the B line, and also present over most of C.

The distribution for the whole autumn season in 1938 is shown in Text-fig. 13*a–d* (comparable with part of Plate XIII of 'Bulletin' No. 8, showing the distribution of Biddulphia patches at that time). The first growths occurred that year in August off Heligoland, with a mean of 143μ (" intermediate "). In September we can distinguish a coastal zone of " large " cells from the Skaw southwards to Borkum (and to the R. Maas by October), with " intermediates " widely scattered on the seaward side and only one sample, near the eastern Dogger Bank, of " small " size. The coastal " large " cells were absent from the Skaw region by October 30th, and receded coastwards near the R. Maas between the 12th and 26th. " Small " cells were recorded in the Southern Bight, stretching from the Sunk Lightvessel nearly to Borkum, where they immediately abutted on the " large " zone, and a predominantly " small " population (mostly showing means > 130μ) extended from the eastern Dogger to the Skaw in the latter part of the month. The possibility of continuity between the two " small " regions arises, but cannot definitely be settled, since the relevant evidence is absent in November.

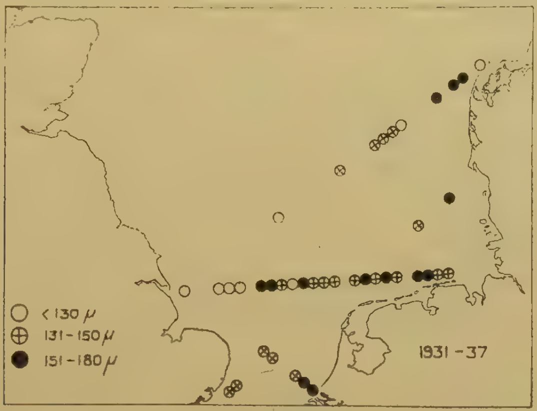


TEXT-FIG. 13.—Showing the positions and mean sizes of all the samples of *B. sinensis* measured during the period August–December, 1938 (*cf.* Pl. XIII of ' Bulletin ' No. 8).

The chief known difference between October and November lay in the reappearance of " large " cells off the Skaw with " intermediates " around them, and the appearance of more " intermediates " on the western B route. The southern " small " cells and the coastal " large " ones were arranged roughly as before, and continued so into December, except in so far as the " small " had by then possibly extended northwards since October 11th (Heligoland Bight), and, as far as the evidence goes, might even have reached the mouth of the Skagerrak from there, although we must remember their presence off the

Skagerrak in October, and we cannot take such an extension for granted. The first "large" cells in the middle of the B route were also obtained in December.

Unfortunately it has not been practicable to obtain such detailed results from the earlier years. One or more samples have been analysed for most of the more obvious patches, and a summary of the resulting data is shown in Text-fig. 14, giving the highest means found on each section during 1931–1937. The means again show the existence of a coastal zone of "large" cells (mean > 150μ), but variously extending along the B route towards the English coast. "Intermediate" cells were common to the seaward side of this zone, including the Southern Bight, and were mixed with the "large" extension along B. "Small" cells were mainly limited to the western Dogger region, and off the Humber (1934–1937), although there were odd sections elsewhere on which a "small" mean was the largest found during the period. It should be mentioned that no means as low as in 1938 were observed during 1932–1937 in the Southern Bight—most were "intermediates"—and there were usually "large" cells nearer the continental coast. On the other hand, rather few measurements were obtained in the south, and "small" patches may have been missed. Another difference from 1938 lies in the smaller size of the "large" means of the earlier years, applying from Skaw down to the Maas. In general, no means as high as 150μ were found from September, 1933, to December, 1935, except near Maas (1934), although twelve different samples were taken along the Frisian Islands then (most of which might have been expected to produce "large" means in 1938), and several more in 1937. On the other hand, larger means were found (particularly in 1937) along the B route than in 1938.



TEXT-FIG. 14.—Showing for the years 1931-37 the highest mean sizes of *B. sinensis* obtained on each 10-mile section of the routes regularly recorded during those years (*cf.* 'Bulletin' No. 3, p. 74, and Plates XXII–XXXVI).

As in 1938, the means and modes of the size curves were in substantial agreement, the higher modes tending to be found nearer the continental coasts.

Significance of the Results.

Whilst we have no directly relevant hydrological information, there seem to be very good grounds for suggesting that such a distribution as is shown here must be closely related to the water types and their movements. The generally close association of the "large" cells with the continental coast suggests an immediate relationship with the normally brackish water to be found there, and the smaller cells are in fact found in regions where the salinity is normally higher. Considering the detailed results for 1938, it seems that we have, in September, to deal with at least two populations of Biddulphia, a coastal and an off-shore one, between which there were usually rapid changes in size; the distribution of the patches in Plate XIII of 'Bulletin' No. 8 would give some support to this. The subsequent size-changes and variations in boundaries are just of the type which might be anticipated if one were, in fact, concerned with the boundaries of the usual water masses in this region. This is particularly so when, in October, we see that quite small cells had appeared (October 11th) in the south, to some extent as if they had the form of a volume of water directed from the region of the English Channel, although extending a little to the west of the usual Channel stream. We have already said that there is no certain connection between these "small" cells and those found later (October 21st–30th) off the Skagerrak, but the latter also occupied an area normally of higher salinity at this time of the year than at others (*cf.* Lucas and Rae, 1946).

From the routine data for 1938 ('Bulletin Hydrographique' for 1938) we do know, in fact, that the salinity of the water containing "large" cells in September was below 34·0‰, whilst as far as the evidence goes, the "intermediate" cells were mainly in water above 34·0‰. By October the salinities at the eastern end of the C line (off the Skagerrak) had increased from 34·0‰, being well over 35·0‰ near the Skaw. Similarly, a patch of high salinity water had appeared in the Southern Bight, again mainly above 35·0‰. It is these salinities which seem to be associated with the "small" cells. Along the coast, however, low salinities were still present, except off Skaw. By November the from-Channel salinities had increased and extended further, in association with the possible spread of the local "small" cell area. Whilst there were still lower salinities on either side of the stream, the water to the east was the lower of the two and contained larger cells than that immediately to the west, where "intermediate" cells were found. The salinity of the water near Skaw, however, had by mid-November decreased to *ca.* 34·5‰ and we see that "large" cells had appeared here once more. In December we recorded the sizes of three groups of cells on the C line, of which the centre produced the only "large" cell-mean (associated salinity 34·45‰), the other two being "intermediates" or "smalls" (salinities 34·85 and > 35·0‰). Similarly, salinities off the Skagerrak were quite high, with "small" to "intermediate" cells, whilst those in the line of the from-Channel flow had increased and extended as, perhaps, had the "small" cells. It is noticeable that along this line (E) the cell size increased, in proportion as the salinity decreased, from south-west to north-east in each month. A particular feature in this region was the coastwise restriction of " large " cells on R between October 12th and 26th, between which dates, too, the high salinity region spread coastwards.

A more precise estimation of the relationships between size and salinity is given when the sizes of the cells nearest to the International stations used earlier by Lucas and Rae (1946, Text-fig. 1) are compared with the 1938 salinities recorded for those stations on the nearest available date. The cells associated with salinities $<34{\cdot}0‰$ averaged 174μ (11) ; those with salinities from $34{\cdot}0$–$34{\cdot}49‰$, 143μ (18) ; those from $34{\cdot}5$–$34{\cdot}99‰$, 134μ (9) ; and those with $> 35{\cdot}0‰$, 123μ (8). Whatever other factors are effective, there can be little doubt of the effect of salinity or some closely correlated factor.

In the light of this relationship we can briefly reconsider the measurements made in 1931–37. The general distribution, in relation to our knowledge of the local salinities in those years (Lucas and Rae, 1946), is clearly in accord with the 1938 findings. Any further remarks, however, must be qualified by the fact that the samples analysed are comparatively few, even in 1937. One feature of 1931–1937 was the smaller total range of mean size compared with 1938. Whilst this will partly reflect the smaller number of samples, the difference in the larger cells, at least, is so consistent as to appear very significant. Again, the autumn of 1935 seems to have had particularly smaller maximum means, even in the coastal zone along the Frisian Islands, and there were no means as high as 150μ from September, 1933, to December, 1935. Both of these features are probably to be associated with the widespread high salinity of that period in the Southern Bight (Lucas and Rae, 1946), although the larger means recorded before and after this period remain still small in comparison with 1938. The latter was itself a year of very high salinity in this area, although the high salinities did not appear until late in the year. Another point concerns the higher means found along the B route, particularly in 1937, in relation to which Lucas (1940 and 1941) has already commented on the annual variations in the westerly spread of *B. sinensis* towards the Humber. This spread was most marked in 1937 and much less so in 1938, and a partly associated factor would appear to be the directions of the from-Channel current as measured at Varne during each autumn (Carruthers, 1935, and Lucas and Rae, 1946, Text-fig. 10). In the autumn of 1937 these were unusually westerly, whilst in 1938 they were decidedly easterly,[1] and the latter condition might reasonably be expected to pen up the large cells of the brackish continental waters more than the former. " Large " modes of $> 150\mu$ also reached far to the west in 1933 and 1936 ; these were also years of marked westerly current at Varne. A further point is in the nature of a problem. Whilst the continental coastal waters are known to be of quite low salinity, moderately low salinities occur also off the British coasts, and one might have anticipated at least some sign of increased local cell-size on the occasions when Biddulphia was present near our coasts. As far as these records go it appears to have been particularly small, which feature, too, may be associated with the tendency for such relatively unusual westerly deviations of Biddulphia patches to be associated with westerly deviations in the from-Channel currents, normally of higher salinity than adjacent waters.

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[1] As before, we are indebted to Dr. J. N. Carruthers for his kind arrangements whereby his current-measurements at Varne may be consulted prior to publication.

This preliminary consideration of size-variation in *B. sinensis* leaves many problems unsolved. For yet another instance, there appears here to be no sign of periodical changes due to an auxospore cycle, such as occurred in *R. styliformis*; perhaps this is related to the frequent production of resting spores in Biddulphia and to a more labile growth habit. Yet certain features emerge which suggest the value of further study, and we are glad to hear that the problem is also being investigated by Mr. R. S. Wimpenny of the Ministry of Agriculture and Fisheries Laboratory at Lowestoft, who has kindly discussed various problems with the writers. One particularly important point concerns the apparent, but by no means certain, differentiation into groups or stocks. No certain signs of difference in shape have yet been detected, and we have no experimental evidence regarding the nature of the response in Biddulphia to external conditions. If it should be almost immediate (*e. g.* within one or two cell divisions), then the apparently consistent difference between a coastal stock and an off-shore stock may be *simply* a reflection of the salinity difference, and the differences in cell-size would not be insignificant to marine biologists even were this so. But we have to consider whether, as probably in Rhizosolenia, cell-size may be not merely a means of patch identification (and this would fail if the salinity response were too immediate), or of salinity indication, but whether it can be a useful " indicator " in the accepted sense, and as we have suggested Rhizosolenia might be.

Careful thought must be given to any use of phytoplanktonts as " indicators," and Gran (1902) has discussed some of the dangers, arising principally from their labile response to the environments. Bearing these points in mind, their very responsiveness may yet prove to be of considerable value, as Gran has suggested for the Ceratia (1902). There is some reason to suppose that this applies to Biddulphia. In his invaluable review of plankton organisms as " indicators," Russell (1939) quoted Wulff (1934) as the authority for using *B. sinensis* as a microplanktonic " indicator " of " pure " English Channel water. Even within the Southern North Sea, the distribution of *B. sinensis* is usually sufficiently widespread (*e. g.* Savage and Wimpenny, 1936, and Lucas, 1940 and 1941) to make this improbable, although we should not for a moment suggest that some *B. sinensis* does not come from the Channel in some years. As far as our evidence goes, however, it often originates within the North Sea around the Heligoland Bight *before* it has been detected in the Southern Bight (*e. g.* on the Hull–Rotterdam route); this appears to have happened at least in 1933, 1934, 1937 and 1938 (Lucas, 1940 and 1941). It is also usually *denser* away from the Channel opening. The present results, however, do show some differences between the populations of Biddulphia. In 1938, at least, we could reasonably, within appropriately limited areas, use " size " as an indicator of differences between a small southern group, possibly influenced by from-Channel water, and a large continental coast group. These groups comprised, in fact, the extremes of size, and it may be well to leave discussion of the " intermediate " sizes until more information is available. Within the Southern Bight we may then have some indications of " Channel " water and " coastal " water. The latter could always be distinguished with ease as far north as the Skagerrak from such types as existed off-shore. Whether the " small " Biddulphia were truly brought in by Channel water, or were caught up in it from some local population, is still uncertain. By their size they appeared to indicate the salt water of the Channel tongue. There have, however, been a number of occasions when, for example, the inflowing Channel waters appear to have cut into the southern Biddulphia patches, the numbers being reduced in the region of the salter water (*e. g.* 1924, in Savage and Hardy, 1935, fig. 35, and 1935 in Lucas, 1940, Plate XXIX ; also 1933 and 1934, in Savage and Wimpenny, 1936, figs. 5 and 14). Such results at least make it less certain that Biddulphia is an indicator of Channel water, even though its size may at times denote the influence of such water. It is interesting that the stocks of " small " Biddulphia were never abundant ones ; we do, in fact, associate its abundance with only moderate or low salinities.

We must remember, however, that even more than with the zooplankton (Rae and Rees, 1947) the absence of an " indication " does not mean necessarily that the thing to be indicated is absent. The possibly direct response of the plant cells to salinity might also have two results ; they might denote by their size-change the adulteration of the water type in which they exist ; and they might in the same manner fail to identify, say, the Channel water owing (as, for example, in 1936) to its dilution to a degree comparable with the salinity of the waters into which it is flowing. Until we know more of the responsiveness of Biddulphia to salinity changes we cannot profitably discuss this further, except to emphasize that these points apply, in theory at least, to the differences discussed above in the sizes of *R. styliformis*. The chief difference is that the latter data suggest some rather more fundamental differences, which to a large extent persisted after mixing. In other words, we can be reasonably certain of the existence of at least two Rhizosolenia stocks in these years, but only, so far, of size differences in Biddulphia.

DISCUSSION.

The type of differentiation within the populations of marine diatoms first demonstrated by Wimpenny and developed here raises a number of issues which may come to interest workers outside as well as within the marine field. Some of these points have been posed by Wimpenny (1946), others in the present paper. In particular we need to know more of the nature of the differences between the different sizes of cells and of the factors influencing their size. Of the latter, Wimpenny has mentioned the possibility of salinity (in addition to temperature and the processes of cell-division), and this possibility has been followed here. Is this (or any similar) influence direct in its nature—a " simple " environmental influence—or is it brought about by " natural selection " ? In the former, the products of cell-division might, for example, more rapidly *decrease* in size in more saline waters as the result of increased salts in the medium although, judging by the common view of the nature of cell-division in diatoms, they could hardly *increase* their size directly by a similar response in waters of lower salinity.

The difficulty might be overcome by the production of spores of one form or another ; we cannot even be sure that auxospore-formation is not influenced in part by the lowering of salinities. A simple " Darwinian " effect, on the other hand, in which one or the other type of cell survived in greater numbers in the appropriate environment, would be generally less difficult to visualize for a population of decreasing or increasing cell-size. A further, and related, problem concerns the presence or absence of sexual processes in these diatoms, about which we know little. As Wimpenny has said, until such points are cleared up, it will be impossible to understand the size-differences adequately, although this should not prevent their use as indicators of essential differences, either physical or biological in their environment.

We have already commented on the apparent relationship between the distributions of the suggested stocks of Rhizosolenia and those of the Sagitta species and of two of the groups of copepods described by Rae and Rees (1947). When discussing the significance of their different copepod groups, they also drew attention to some resemblances between the distribution of *Corycaeus anglicus* and that of *B. sinensis*, referring also to *Phthisica acaudata* (*cf.* also Marshall, 1948). If we accept, for the moment, the two main divisions into which Biddulphia has here been separated, it is evident that the coastal zone corresponds closely with that of the denser concentrations of Corycaeus in most years, although it contains by no means necessarily the densest concentrations of Biddulphia—merely the largest cells on most occasions. This is approximately the Flemish Coastal Water, etc., of Russell (1939), although it will be remembered that Corycaeus, as well as Biddulphia, is also found outside that zone ; whilst Biddulphia can be distinguished in the two types of water, we only as yet know of numerical differences for Corycaeus. *Phthisica*, on the other hand (Henderson and Marshall, 1946, and Marshall, 1948), tended usually to be more abundant a little away from the continental coast and, in contrast, it was most abundant on the R line, although it extended to the Skaw at times. Its distribution resembled more that of the off-shore Biddulphia, and its maximal areas in 1938 in some respects tended to agree more with those of the smaller (but not necessarily the smallest) diatoms, although altogether it was far more extensively distributed in our records, perhaps sometimes to the east of the expected Channel stream.

These points can more suitably be discussed later when the plankton is considered as a whole, but it is now possible to add a little to the picture drawn from monthly records by Rae and Rees, which so strikingly confirmed with different material the generalized picture drawn by Russell (1939, fig. 5). Over the basic picture of an "*elegans*" area and a "*setosa*" area can now be seen, we believe, the phytoplankton counterparts of "small" and "large" Rhizosolenia, although the last has generally a less extensive overall distribution than *S. setosa*. Rae and Rees, with their copepod equivalents, distinguished for 1938–1939 the "Isias-Labidocera" and the "Corycaeus" regions of the "setosa" area (in addition to the "Euchaeta-*C. hyperboreus*" region off the Norwegian coast), and in "large" Rhizosolenia and "large" *B. sinensis* we now see the phytoplankton counterparts of these. The smaller *B. sinensis*, to our mind, help to fill in the picture, and are not least interesting in including that section of the Biddulphia population (largely, but not entirely "intermediate"), which in some years (Lucas, 1940 and 1941) becomes involved with the main Rhizosolenia patch of the South-west Dogger Bank Swirl. The smallest of all the Biddulphias, on some occasions at least, appear to be related to the from-Channel Biddulphia of Russell's figure. If, in fact, they are merely influenced by Channel water, whilst truly a local stock, then we may have an explanation of the shift in focus of "small" cells from the "off-Humber" region in some early years (1934–1937) to further south and east in 1938, following the marked easterly deviation of the Channel current in 1938 after several years of more or less westerly trend.

The inter-relations of these four groups, depicted by their varying annual boundaries (together with those of their planktonic associates), may further advance our knowledge of the complicated water movements in the North Sea. This possibility is emphasized when we compare the impression gained so far of the mean distribution of these groups with that of the depth contours of the North Sea. The "small" Rhizosolenia area is not dissimilar from that of the 60–200 metre region of the North Sea, and the smallest of all cells (Text-fig. 3) were very closely grouped in the 80–200 metre region (The Gut). Normally, the large Rhizosolenias occupied water of less than 60 metres depth, penetrating once over the 200 metre deep off Norway, and mixing with the small ones over 60–80 metre areas north-west of the Dogger Bank. The "large" Biddulphias, in turn, scarcely spread from the 0–20 metre coastal region off the continental coast (although we did not record them over the corresponding, but limited zone off England), except at times along the B route (p. 159). "Small" and "intermediate" cells were present here, but spread at times over most of the water up to 40 metres in depth, and even, in the north-east, to 60 metres. These last tended to be quite small, although infiltrated at times by large cells, and the smallest of all were found around the 40–60 metre gully running north-eastwards from the Dover Straits. With individual variations these relationships apply to other planktonts and must be brought about by the water-movements, as, in part at least, may have been some of the contour lines of the bottom itself.

In conclusion, the existence of such marked differences between the various populations of *Rhizosolenia styliformis* and *Biddulphia sinensis* suggests, not only that such features may characterize other diatoms, but that similar ones may be found in other plankton organisms which have an apparently wide distribution, and particularly if they show signs of having more than one focus of distribution. Among possible examples are *Nyctiphanes couchii*, *Centropages typicus*, and *Themisto gracilipes* Norman, which have foci in the north-western and in the central North Sea. Another example lies in those Dinoflagellates, particularly *C. fusus*, which have their densest zones in the north-west and in the south-east, and it is hoped later to investigate more fully the differences existing between these populations.

SUMMARY.

1. More than eighteen thousand cells of *Rhizosolenia styliformis* Brightwell and nearly twenty thousand cells of *Biddulphia sinensis* Greville have been measured from the continuous plankton records obtained in 1931–1939.

2. For the whole North Sea in 1938–1939 the Rhizosolenia data strongly suggest subdivision into at least two populations: a north-western one of smaller cell-size and a south-eastern one of larger cell-size, sometimes abruptly separated, but between which there was mixing in the autumn. These areas may be compared with the " *Sagitta elegans* " and " *setosa* " areas of other workers, and are areas generally of more and less salt water respectively.

3. The data for the Southern North Sea appear to confirm and extend Wimpenny's account of the auxospore cycle during the years 1932–1939, and show that the smaller of the " large " cells (mainly the older phases of the auxospore cycle) tend to be relatively more abundant around the western Dogger Bank than elsewhere in the Southern North Sea.

4. The primary size-modes of the " large cell " population are usually well above 40μ, whilst those of the " small cell " population are usually below 40μ. The possible admixtures of the two are discussed, together with their relationships to Wimpenny's suggested varieties and to their environment.

5. The sizes of *Biddulphia sinensis* permit distinction between a large-celled population along the continental coast, a more widespread one of intermediate cell-size, and one of small cells which, in 1938 at least, may have been influenced by the stream issuing from the English Channel mouth.

6. Evidence is given for a marked relationship between Biddulphia sizes and salinity, the smallest cells being found in the saltest water and the largest ones in coastal water. This association may have brought about certain annual differences in distribution.

7. The relationships of these results to those of workers in this and other laboratories are discussed, particularly in relation to the " Indicator " concept.

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APPENDIX: TABLES I AND II.

TABLE I.—*Giving the dates, chart reference numbers or letters, with station code numbers for the original sources (Lowestoft or Hull), and numbers of cells of* R. styliformis *measured in each of the samples shown in the charts of Text-fig.* 2a–h. *Lowestoft samples are denoted " L " and Hull samples " H." The station codes refer respectively to the lists given by Wimpenny* (1936 *or* 1946) *and in 'Hull Bulletin' No.* 2. *The letters " N " and " S " before sample reference numbers or letters indicate north-western or south-eastern samples respectively. The samples for which size-frequency curves are illustrated in Text-fig.* 2. *are shown thus, NA, NB, S3, S4, etc., whilst those for which some other size-curve has been considered adequate representation in that figure are shown here thus,* ^{4}*S, etc., the prefix denoting the number of the typical curve (see legend for Text-fig.* 2).

Year.	Month.	Sample No. or letter.	Source.	Station code.	Cells measured.
1932 (Chart 2*a*)	IV	NA	L	E3	100
	V	NB	L	B2	50
	VI	NC	L	D12	100
	VIII	ND	L	E4	100
	IX	S1	L	0–20/2	100
	X	S2	L	HQ	100
	X	S3	H	7B7	300
	X	S4	L	J26	100
	IX	S5	H	5C5	100
	X	S6	H	7B8	210
	X	S7	L	J12	100
	X	S8	L	J32	100
	X	S9	L	J19	100
	X	S10	L	J20	100
	X	S11	L	J22	100
	XI	S12	H	6C22	102
	XI	S13	H	6C23	100
1933 (Chart 2*b*)	V	NA	L	E5	100
	V	NB	L	B19	100
	V	NC	L	B9	100
	VI	ND	L	E6	100
	V	S1	L	C20	100
	VII	S2	L	F5	100
	IX	S3	L	J5	100
	X	S4	L	K28	100
	X	^{4}S	L	L35	100
	X	S5	H	15C9	123
	V	S6	L	C10	100
	IX	S7	H	20B1	194
	X	S8	L	K1	100
	X	^{8}S	L	K13	100
	X	S9	L	L15	100
	X	^{9}S	L	L30	100
	X	S10	L	L9	100
	X	^{10}S	L	K12	203
	XI	^{10}S	L	0–25/8	102
	XI	^{10}S	L	0–25/9	300
	XII	^{10}S	L	0–29/T	100

TABLE I—*cont.*

Year.	Month.	Sample No. or letter.	Source.	Station code.	Cells measured.
1934 (Chart 2*c*)	V	NA	L	C19	100
	V	NB	L	E7	100
	VI	NC	L	E5	100
	X	ND	L	M3	100
	VI	S1	L	E17	100
	VII	^{1}S	L	G5	100
	VIII	S2	H	35B2	50
	VIII	S3	H	35B11	50
	IX	S4	L	L17	100
	IX	S5	H	37B2	100
	IX	S6	H	37B5	100
	X	S7	L	M21	100
	X	^{4}S	L	M14	100
	XI	^{7}S	L	0–35/6	100
	XII	S8	H	46B2	50
1935, April–Sept. (Chart 2*d*)	IV	NA	L	E8	100
	IX	S1	L	N6	100
	IX	^{1}S	L	N5	300
	IX	S2	L	N12	100
	IX	S3	H	59B1	100
	IV	S4	H	52B8	50
	V	S5	L	F7	100
	VI	S6	L	G27	100
	IX	S7	H	38C6	200
1935, Oct.–Dec. (Chart 2*e*)	X	S1	L	O15	100
	X	S2	H	61B3	200
	X	S3	L	O16	100
	XI	S4	L	1215	100
	XII	S5	H	40C12	66
	X	S6	H	60B15	104
	X	S7	L	O13	200
	X	^{7}S	L	P11	200
	X	S8	L	O34	100
	X	S8	L	O34	100
	X	S9	H	61B9	300
	X	S10	H	63B8	200
	X	S11	L	P21	100
	X	^{11}S	L	P14	100
	XI	^{7}S	L	Q24	100
	XI	^{7}S	L	R3	100
1936 (Chart 2*f*)	V	NA	L	G15	100
	V	NB	L	G3	100
	VI	NC	L	E9	100
	V	S1	L	G39	100
	XI	S2	H	85B5	201
	XI	S3	L	Q18	100
	VIII	S4	L	J17	100
	XI	S5	L	P22	100
	XI	S6	L	Q12	100
	XI	S7	L	Q30	100
	XII	S8	H	88B9	150

TABLE I—*cont.*

Year.	Month.	Sample No. or letter.	Source.	Station code.	Cells measured.
1937*A* April–Sept. (Chart 2*g*)	VIII	NA	L	E10	100
	II	S1	L	O–IV/F6	100
	IV	S2	H	57C11	98
	IV	S3	L	0–VI/F6	100
	VI	S4	L	H19	100
	IX	S5	H	103B7	100
	V	S6	L	F21	100
	VIII	S7	L	L31	100
	VIII	S8	L	L30	100
	VIII	S9	H	61C10	102
	IX	S10	H	102B9	100
1937*B*, Oct.–Dec. (Chart 2*h*)	X	S1	H	106B5	250
	X	S2	L	M10	100
	X	^{2}S	L	M18	100
	X	S3	L	M19	100
	X	S4	H	107B4	100
	X	S5	H	108B10	100
	X	S6	H	63C7	100
	X	S7	L	M16	100
	X	^{7}S	L	M17	100
	X	^{7}S	L	N13	100
	X	S8	L	N29	100
	X	S9	L	M15	100
	X	^{9}S	L	M21	100
	X	^{9}S	L	M37*a*	100
	X	S10	L	M24	100
	X	S11	L	M23	100
	X	^{11}S	L	M26	100
	X	^{11}S	L	N16	100
	X	S12	H	107B7	67
	X	S13	L	M11	100
	X	^{13}S	L	N25	100
	XI	^{8}S	I	P1	100

TABLE II.—*Giving the dates, chart reference numbers, with station code numbers for the original sources (Lowestoft or Hull), and numbers of cells of* R. styliformis *measured in each of the samples shown in the charts of Text-fig.* 6a–l. *Lowestoft samples are denoted " L " and Hull samples " H." The station codes refer respectively to the lists given by Wimpenny* (1946) *and in 'Hull Bulletin' No.* 7.

Year.	Month.	Sample No.	Source.	Station code.	Cells measured.
1938	I	1	H	1K4	104
(Chart 6*a*)	II	2	H	1L8	105
	I	3	H	1K22	100
	II	4	H	1S24	100
	II	5	H	66C23	79
	II	6	L	D/F6	100
	III	7	L	E/F5	100
(Chart 6*b*)	V	1	H	2A23	60
	V	2	H	2A18	100
	V	3	H	4M6	100
	IV	4	H	68C8	60
(Chart 6*c*)	VII	1	L	E11	271
(Chart 6*d*)	IX	1	H	74C5	150
	IX	2	H	75C23	100
	VIII	3	H	119B6	100
	IX	4	H	121B2	100
	IX	5	H	23E23	127
(Chart 6*e*)	X	1	H	11M8	99
	X	2	H	75C5	100
	X	3	H	124B8	100
	X	4	H	75C33	100
	X	5	L	P11	100
	X	6	L	P13	100
	X	7	L	P27	100
(Chart 6*f*)	XI	1	H	12M9	100
	XI	2	H	13M17	100
	XI	3	H	77C23	100
	XI	4	H	125B7	100
	XI	5	H	25E24	50
	XI	6	L	Q16	100
	XI	7	L	Q8	100
(Chart 6*g*)	XII	1	H	14M12	103
1939					
(Chart 6*h*)	I	1	H	16K20	100
(Chart 6*i*)	III	1	L	E12	100
	III	2	H	18K17	100
(Chart 6*j*)	IV	1	H	13A23	100
	IV	2	H	13A20	100
	IV	3	H	21M4	100
	IV	4	H	20M12	100
	IV	5	H	19K19	100
	IV	6	H	15Z23	100
(Chart 6*k*)	V	1	H	14A23	100
	V	2	H	22M6	100
	V	3	H	21K21	100
(Chart 6*l*)	VII	1	H	4V22	100
	VII	2	H	134B11	100

[*Hull Bulletins of Marine Ecology, No. 13, Vol. II, pp.* 173–213, *Plates LXXXIX–CVIII, August, 1948.*]

CONTINUOUS PLANKTON RECORDS:
ZOOPLANKTON (OTHER THAN COPEPODA AND YOUNG FISH) IN THE NORTH SEA, 1938-1939

BY

N. B. MARSHALL, M.A.

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INTRODUCTION.

This paper describes results obtained in the extended plankton recorder survey of the whole North Sea from January, 1938, to August, 1939. It should be compared with reports covering a similar period for the phytoplankton ('Bulletins' Nos. 8 and 9, Lucas, 1941, 1942), the Copepoda (' Bulletin ' No. 11, Rae and Rees, 1947) and the ' Young Fish ' (Stubbings and Henderson, in preparation). The plankton for the Iceland line in 1939 is described in ' Bulletin ' No. 10 (Lucas, Marshall and Rees, 1942). The writer took up war service in the forces while the present paper was in preparation, and its completion had to be delayed until a suitable opportunity arose after the war.

We have not been able from this relatively limited period to draw any conclusions regarding long-term changes in the zooplankton, but we have continued to plot the monthly averages of plankton catches on the Bremen, Copenhagen and Rotterdam lines from Hull so as to link up this work with that begun in the earlier Southern North Sea survey, described in 'Bulletin' No. 6 (Henderson and Marshall, 1944).

Besides extending our investigations to cover the whole of the North Sea we have been able to give more detailed month by month analyses of the plankton. In particular, we have concentrated on the "indicator" species, *i.e.* those which indicate the main water movements. Since the Plankton Recorder collects samples at a constant depth of 10 metres it is always necessary to consider the possible effects of diurnal and seasonal variations in vertical distribution.

The recorder material does not lend itself readily to a statistical treatment of this last problem, although there has been some brief discussion of it in 'Bulletins' No. 1 (Hardy, 1939, p. 48), No. 4 (Rae and Fraser, 1941, p. 180), and No. 6 (Henderson and Marshall, 1944, p. 257). Such evidence as we have suggests that its effects, at least in the shallower waters, are comparatively small, although undeniable, in comparison with the great seasonal variations in total numbers which occur. In the euphausians, however, vertical migration may seriously bias collections made at 10 metres (see p. 181).

The routes sampled in each month have been set out in 'Bulletin' No. 7 (Hardy, 1941) as a series of key charts showing the record letter together with the date, the time of the beginning and end of the record, and the number of miles sampled. Full reference is made to the occasions on which certain lines deviated from the normal course, but special attention must be drawn to the S line running from Hull to Oslo or Christiansand which was only in operation from February to August in 1938: the northern end of this line passed through parts of the Skagerrak deep which we were not able to sample again. Valid records are shown on these maps as continuous lines, while "qualitative" records (*i.e.* records or parts of records having some slight defect which might have led to a loss of plankton) are shown as dotted lines. Although the "qualitative" records cannot be given the same validity as a normal record, the losses are not likely to have been serious for most purposes, and they have been treated in the present paper as providing an adequate picture of the quantitative distribution.

METHODS OF ESTIMATION.

Two methods have been used for finding the total number of organisms on each ten-mile "block" of silk ('Bulletin' No. 7, p. 3).

The smaller and more numerous organisms, *i.e.* Limacina, Oikopleura, cladocerans, lamellibranch larvae, cyphonautes larvae, echinoderm larvae, and decapod larvae when very abundant, were estimated for each ten-mile "block." The numbers seen in two evenly spaced microscope traverses across the graduated and plain silk were multiplied by a factor, depending on the length of silk used in sampling ten miles of sea. Henderson and Marshall (1944) have already shown that this method gives a reasonable approximation to the true value except when the plankton is very unevenly clumped together on the silk, and this we still find to be a fairly rare occurrence.

Larger organisms such as the Chaetognatha, decapod larvae (when not too numerous), amphipods, mysids and euphausians, were counted directly on the silk by the unaided eye. The procedure for identifying the *Sagitta spp.* was made dependent on the total numbers present. For values ranging from 100–200 per block not less than one-fifth of the total were examined. When the numbers were above this range not less than one-tenth were examined. For the range below 100–200 from a fifth to the whole of the catch was examined. When the species were mixed the greater part of the catch was examined in order to obtain an estimate of the proportions of each species. It was not possible to identify all specimens, some even of the larger ones being too damaged. In general, however, all but the smallest stages were identifiable.

FORM OF PRESENTATION.

Two methods are adopted for showing the numbers and distribution of the organisms.

For the smaller and more numerous forms, and the amphipods, a series of symbols was devised, each symbol representing an arbitrary range in numerical value. The symbols for echinoderm larvae, cyphonautes larvae, lamellibranch larvae, Oikopleura, Podon and Evadne represent the numbers per mile for each ten-mile block, while the less numerous decapod larva and amphipods have been shown as total numbers per ten miles. All of these organisms have a well-marked seasonal occurrence, and in consequence we have only thought it worth while (with the exception of the amphipods) to show the more important months of the year in each series of charts.

A more precise system was used for the euphausians, chaetognaths and Limacina. The euphausians are shown on two series of charts, each symbol representing both the species and the numbers per ten miles. The numbers within the different symbols for *Sagitta spp.* also refer to the numbers per ten miles, but are approximated to the nearest ten or hundred. The more numerous Limacina, however, are shown in numbers per mile per ten-mile block, also to the nearest ten, hundred or thousand. For further details the reader is referred to the charts (Plates LXXXIX–CVIII) and the legends on p. 214.

GENERAL DISTRIBUTION.

Sagitta spp. (Plates LXXXIX–XCI and XCVII.)

It was not possible to identify these specifically from January to June in 1938, when the plankton was scraped off the rolls and Sagitta was badly damaged. From July, 1938, onwards specific identifications were made, *Sagitta elegans* Verrill and *S. setosa* J. Müller being the only common species at 10 metres depth. *Sagitta serratodentata* Krohn was also found and is dealt with later in this section.

Sagitta elegans Verrill and *Sagitta setosa* J. Müller.

The occurrence of *S. elegans* is shown on the charts by white numbers within blacked-in circles, and that of *S. setosa* by black numbers within plain circles. Where the two species occurred together modifications of these symbols have been used which are self explanatory (see scale and legends).[1] In general when the proportions of either species constituted between one-third and two-thirds of the total catch equal mixing has been assumed, while when either reached proportions over two-thirds it was considered the dominant form. The number printed within each symbol represents the number recorded within ten miles.

As would be expected from the earlier work of Meek (1928), Fraser (1937, 1939) and Furnestin (1938), together with Russell's (1939) summary and synthesis, *S. elegans* was the dominant form in the north-western area, while *S. setosa* characterized the rest of the North Sea (except the north-eastern part off the Norwegian coast). However, whereas it was unusual to find *S. setosa* in truly north-western waters, *S. elegans* occurred not infrequently in the "*setosa*" area.

The charts show that *S. setosa* was much more numerous than *S. elegans* at 10 metres, and that particularly during the winter months the latter species declined rapidly, having been most abundant from July to October in 1938. *S. setosa*, on the other hand, did not decline until the end of the year, as was shown by the continued presence of young stages. Russell's results (1933) for the Plymouth area were similar. He found that *S. elegans* apparently died down in September after the last spawning period, but the decrease in the *S. setosa* population (also taking place after the last spawning) did not occur until November. As far as the two years of this survey can be compared it would seem that *S. elegans* was rather more abundant in 1939 than in 1938, while *S. setosa* was the reverse of this; the graphs in Text-figs. 1–3 labelled *Sagitta spp.* (but made up almost entirely of *S. setosa*) clearly illustrate this decrease on the Bremen, Copenhagen and Rotterdam lines from Hull.

Returning now to a consideration of each species, in July, 1938, *S. elegans* was best developed in the more extreme north-western waters, but as the season advanced it became more abundant in southern Scottish waters, occupying in our September records a north-western area which was sharply separated from the waters containing *S. setosa*. During October and November the pure "*elegans*" area appeared to expand both eastward and southward, whilst there was also a progressive mixing between the two forms which was most marked along the Forth–Skaggerrak route and consisted in the eastward penetration of very sparse populations of *S. elegans* into the "*setosa*" area. Later, owing to the decline in the Sagitta populations, the boundary between the two species became even less clearly defined, and it was not until July and August in 1939, when the stocks increased once more, that it again became evident in the north-west.

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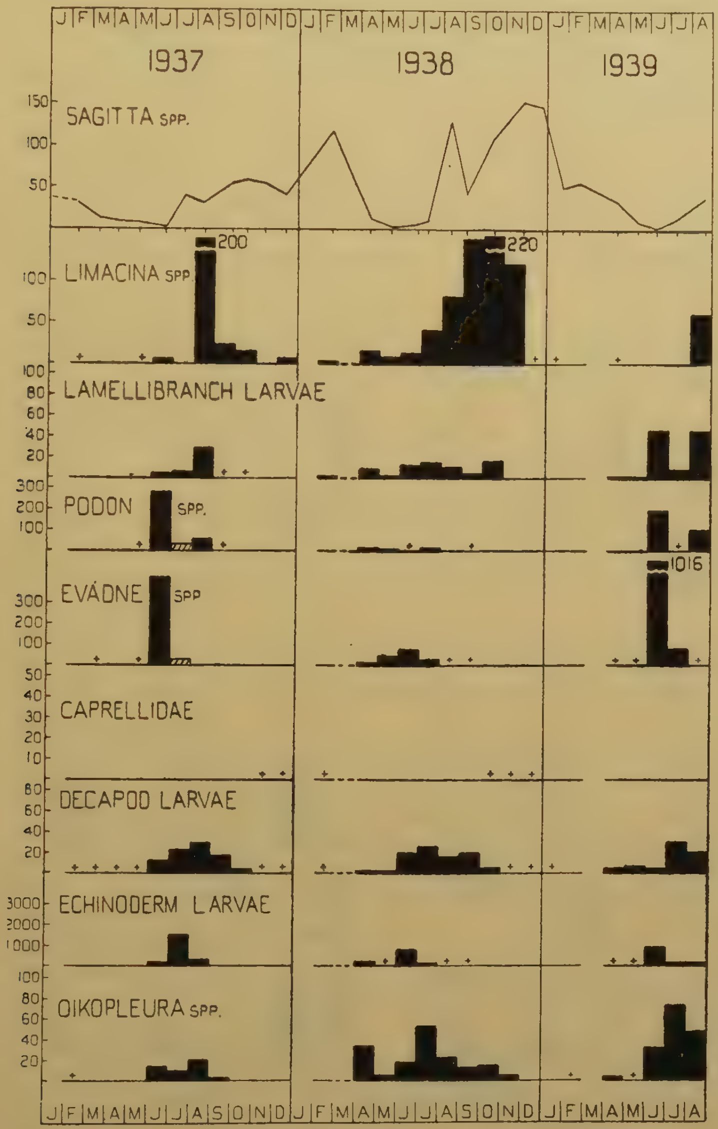
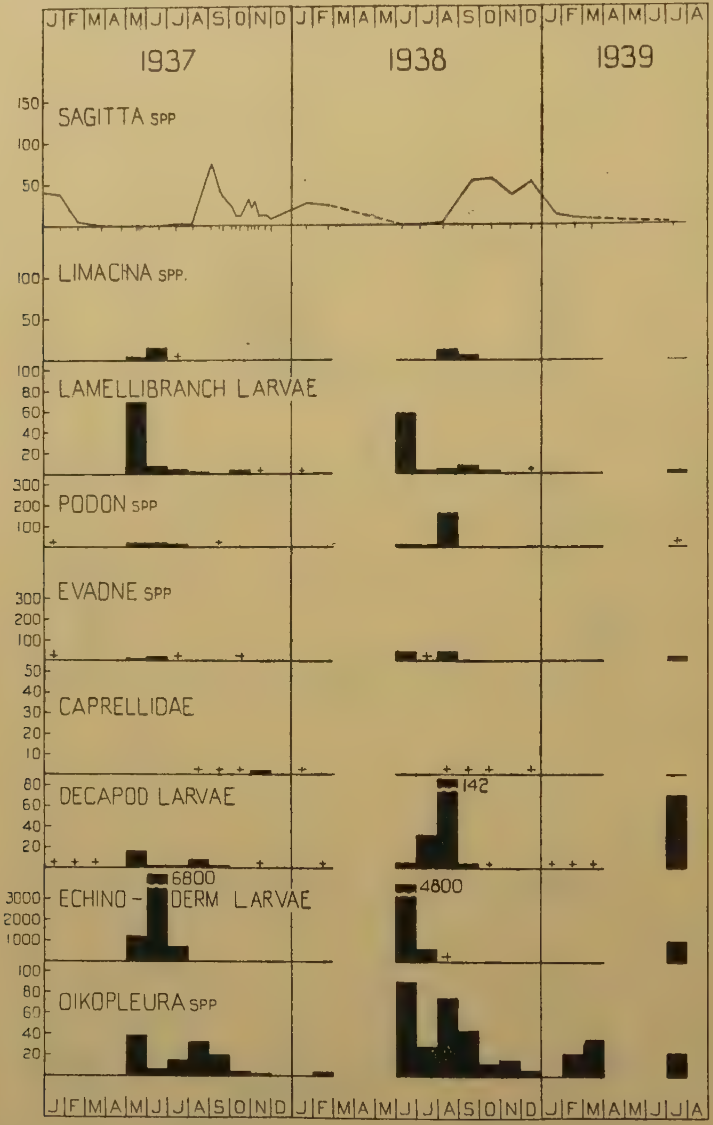
[1] There is an error in the October chart on Plate XC. Two Pentland Firth—Bergen records were taken during this month, both yielding pure populations of *S. elegans*. The upper record has been shown by mistake to represent a pure *S. setosa* population.

Besides being so characteristic a form in Scottish waters, *S. elegans* was usually present in the Humber–S.W. Dogger Bank region, and often occurred in the mouth of the Skagerrak. It appeared off the East Anglian coast in December, 1938,



Text-fig. 1.—Graph and histograms showing the average numbers of the commoner zooplankton forms (other than Copepoda) per ten-mile block on the Copenhagen line for each month from January, 1937, to August, 1939 (for comparison with Text-fig. 1 of 'Bulletin' No. 6). The dates of the records are denoted by small vertical strokes below the base-line of the Sagitta graph; elsewhere the absence of a record in any month is shown by a gap in the base-line. Records of less than half of the normal length have been discarded and denoted by broken base-lines in the histograms. The shaded histograms denote Cladocera *gen. indet.*

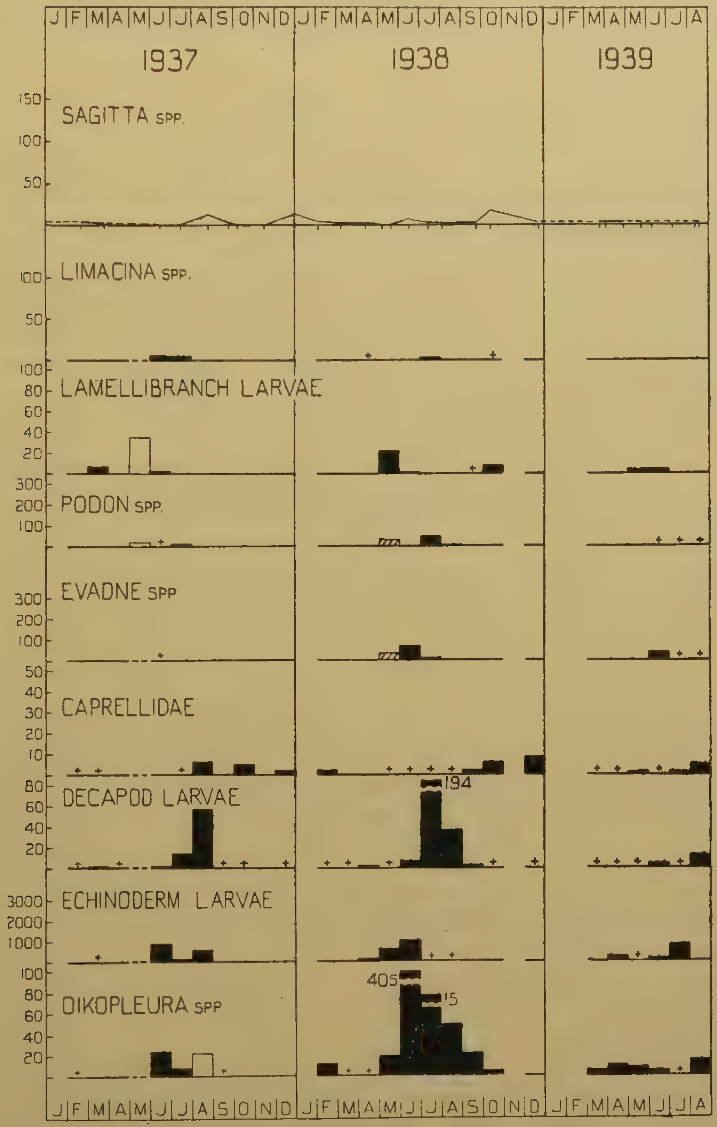
and spread eastwards across the Southern Bight during the spring ; this movement apparently culminated in its becoming more frequent in our catches off the Heligoland Bight in May, 1939.



Text-fig. 2.—Graph and histograms showing the average numbers of the commoner zooplankton forms (other than Copepoda) per ten-mile block on the Bremen line for each month from January, 1937 to August, 1939 (for comparison with Text-fig. 2 of ' Bulletin ' No. 6). See also legend of Text-fig. 1.

Sagitta setosa may be dealt with more briefly. It was the typical form in the waters outside the north-western area, but we found it to be less abundant in the

Southern Bight and the Heligoland Bight than in the more central regions, and usually very scarce along the west coast of Norway. Off the Norwegian coast it was only recorded for 1938 in December, while few specimens were taken from March to June in 1939. During July and August of 1939, however, it became



TEXT-FIG. 3.—Graph and histograms showing the average numbers of the commoner zooplankton forms (other than Copepoda) per ten-mile block on the Rotterdam line for each month from January, 1937 to August, 1939 (for comparison with Text-fig. 3 of 'Bulletin' No. 6). See also legend of Text-fig. 1 (open histograms are used twice where the numbers from less than one-half of a record were even higher than those on either side).

quite abundant on the eastern half of the Pentland Firth–Bergen line, which would suggest a northward extension of the more southerly waters in which the species thrives.

Sagitta serratodentata. Krohn.

This species was only recorded off the Orkneys in April and May, 1939.

Pteropoda. (Plates XCII, XCIII and XCVII.)

Limacina: Although complete certainty of identification is not possible with our material, by far the greater part of the catches must have consisted of *Limacina retroversa* (Fleming). The distribution in both 1938 and 1939 showed certain characteristic features which are probably repeated with variations every year. These give us for the first time a basis for comparison with subsequent surveys, and certainly throw the earlier results for the Southern North Sea (Henderson and Marshall, 1944) into clearer perspective. The chief of these features was the great development of this form in the north-west from May to October in 1938 and from May until the end of the survey in August, 1939. The presence of a fairly abundant Skagerrak population in August, 1938 and July, 1939 should also be noted, while the development of a dense patch off the North Jutland coast in October, 1938, the beginning of which is suggested by the September records, was an outstanding feature. In the Southern North Sea, as we found in the earlier survey, it was most frequent and abundant on the line running from the Humber to the Skagerrak. The histograms of monthly averages on this Copenhagen line (Text-fig. 1), when compared with the earlier figures of 'Bulletin' No. 6 (Text-fig. 1), show it to have reached a maximum in October, 1938; this high figure was almost entirely due to the development of the North Jutland patch referred to earlier, and it should be noted that this part of the line was not recorded prior to 1937. The previous highest, August, 1937, was based on a patch well to the west of this one. From October onwards the populations died down quite rapidly, and only scattered traces of the species were to be found in the winter and early spring months.

Clione limacina (Phipps): Only one adult was taken during this survey, off the Norwegian coast in September, 1938. The remainder were young stages from 3–8 mm. in length.

The first records for Clione (July, 1938) extended over a very wide area, from the Orkney–Shetland region to the off-Norway waters. They were commonest in the central area of the Northern North Sea. It became less frequent in the latter region in August and commoner in the north-west, where an odd specimen appeared as far south as the latitude of the Forth. It was not until September, however, that this southerly spread resulted in Clione becoming common in southern Scottish waters, and even so it did not appear on the Leith–Hamburg route until October. This north-western population had almost disappeared from our records in November, and by December Clione was only recorded off the Humber. From January to March in 1939 odd records on the Hull–Bremen route strongly suggest that there had been an easterly translation of the Humber population across the Southern Bight.[1] In the summer of 1939 it did not become common in northern waters until August, the distribution for this month being similar in some respects to that in July, 1938.

Euphausiacea. (Plates XCIX and C.)

The euphausians, in particular, make extensive vertical migrations, and allowance must be made for these, even in the shallower waters, before the significance of the records is considered. We might, for example, expect our results to give a truer picture of the autumn and winter distributions, when the sections of lines sampled in darkness are lengthened, than of distributions in spring and summer when these sections become shortened. The parts of lines taken between sunset and sunrise are shown in ‘ Bulletin ’ No. 7, and a comparison of them with the distribution of the four main euphausian species does indicate that the greater part of our catches were taken at night.

The recorder material does not lend itself readily to a statistical treatment of the night and day catches, since along our lines, most of which extend right across the North Sea, differences in horizontal distributiona certainly occur, and it is not easy to separate the effect of this spatial factor from that due to vertical migrations. In order to minimize the spatial effect as much as possible the North Sea was divided into a north-western area, a north-eastern area and a southern area. The lines which cover the north-western area are : the entire Leith–Lerwick line, the western half of the Pentland–Bergen line and the first 18, 12 and 10 blocks (at the British side) of the Pentland–Hamburg, Leith–Copenhagen and Leith–Hamburg routes respectively. The north-eastern area is covered by the last 10 blocks of the Pentland–Bergen and Hull–Stavanger routes and the last 14 blocks of the Leith–Copenhagen route. The southern area includes the Hull–Copenhagen line and all lines or parts of lines to the south of it. For each of these areas the number of 10-mile blocks sampled by day and night in each month has been obtained, together with the frequency of occurrence of the euphausians (*i.e.* the number of different 10-mile blocks on which euphausians were found). From these data the average proportionate frequency for night and day has been calculated for the entire survey. Finally the results have been expressed as average night/day frequency ratios and these are set out in the following table :

North-western Area :	*Average night/day frequency ratio.*
Total adult euphausians	2·3
Total larval euphausians	2·1
Adult *Thysanöessa inermis*	1·9
Larval *Thysanöessa inermis*	2·2

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[1] The young stages taken in the Southern North Sea were larger than those recorded earlier in the season in northern waters, with the exception of the single specimen taken off the Norwegian coast in September, 1938.

	Average night/day frequency ratio.
North-eastern Area :	
Total adult euphausians	6·0
Total larval euphausians	2·9
Adult *Meganyctiphanes norvegica*	7·0
Larval *Meganyctiphanes norvegica*	1·8
Adult *Thysanöessa raschii*	3·5
Larval *Thysanöessa raschii*	2·2
Southern Area :	
Adult *Nyctiphanes couchii*	4·8

For the north-western area *T. inermis* has been selected for special attention since it is by far the most common species. Similarly Meganyctiphanes and *T. raschii* almost entirely make up the north-eastern stock of euphausians, while Nyctiphanes was the only euphausian to be recorded in the southern area.

Thus, the individual species of adult euphausians may occur from two to seven times as frequently by night as by day, whereas the young stages occur approximately twice as frequently by night. This latter result was not unexpected, since Einarsson (1945) has shown that in general the earlier larval stages of euphausians inhabit the upper water layers, and only begin to seek deeper levels at later stages of their development.

In order to rule out this diurnal effect as far as possible, conclusions have been particularly based on the presumably more reliable night records, which at this level usually sampled the area relatively well, and attention has been paid to the larger scale differences from month to month which cannot be correlated with the smaller differences due to night and day sampling, although here we must also allow for seasonal migrations. Furthermore much of this work has been concerned with the young stages, which we have already shown to exhibit less diurnal effect than the adults. We feel that, in spite of the limitations, the results of this survey have for the first time given us, over a large area and in one period, a useful conception of the euphausian populations, both corroborating and extending the recent work of Einarsson (1945).

A remaining point concerns the separation of the older from the younger stages. It has not been possible to determine the exact stage of development attained by most of the specimens, but merely to place them within the categories adults[1] and larvae. This means that there may be a considerable age-range within each category, since for each of the principal species all stages from young Calyptopis to moderately large adults have been recorded by us in the North Sea.

The comparatively long larval life of euphausiaceans in these waters raises the important question of whether the presence of larvae, in the widest sense, may be due at any time to breeding within the same or a neighbouring locality, or whether it may be the result of drift from distant spawning grounds. By combining the available evidence regarding the age of the major patches of larvae with other appropriate evidence (*e.g.* the occurrence of spermatophores), suggestions are made regarding some of the more important spawning grounds. It is hoped that the data from post-war surveys will enable these suggestions to be checked and perhaps extended. In brief, however, they suggest that for the North Sea the chief spawning areas for *M. norvegica* are in the Norwegian waters, as also *T. raschii*; while *T. inermis* appeared to breed not only in these waters but more extensively off Orkney–Shetland and the Moray Firth. The young stages of *N. couchii* were found in most parts of the North Sea, except the Norwegian waters.

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[1] (i.e., having the adult form of telson and antenna).

Meganyctiphanes norvegica (M. Sars). (Plates XCIV–XCVII.)

In accordance with Einarsson (1945), the main swarms of adults were found over the deep waters off the Norwegian coast and in the mouth of the Skagerrak; the highest numbers in both regions were taken during the summer. Our results suggest that they were commoner in the former region, but the Skagerrak was less adequately sampled, particularly during the hours of darkness. In Scottish waters they were most frequently to be found during the winter months but always in small quantities. Throughout the survey the Firth of Forth–Skagerrak line marked the southern limit in our records.

In 1938 the larvae were rare and only found in the north-west in August and off the Skagerrak in October. In 1939, however, they began to appear off the Norwegian coast in May following the recording of females with spermatophores. They persisted there until the end of the survey in August, and were most abundant in June and July in keeping with the earlier work of Hjort and Ruud (1929). Our results certainly suggest that 1939 was the more successful brood year. In the Faroe–Shetland Channel larval Meganyctiphanes were also very abundant in March, 1939 (Lucas, Marshall and Rees, 1942).

Nyctiphanes couchii (Bell). (Plates XCIV–XCVII.)

Although Nyctiphanes was the most widespread of the euphausians, it was never found in such dense swarms as were sometimes typical of the other three common species. The adults were most abundant in the north-western area, but quite common over the Dogger Bank, in the Southern Bight, and around the entrance to the Skagerrak. In German waters they were taken less frquently, and off the Norwegian coast they were only recorded in December, 1938 and in April and May, 1939. As a whole, they were very restricted in the spring, and commonest in the north-west in the summer.

The first record for the young stages was obtained off the Humber in July, 1938, whereas the first of the north-western larvae were found in the Orkney–Shetland region in August. In September the young Nyctiphanes were only found in the Scottish area, but in October and November there occurred a striking expansion of the distribution of both larvae and adults to the south and east. Eastwards larvae and adults almost extended to the mouth of the Skagerrak, while to the south the larvae were particularly common over the south-west and north-east slopes of the Dogger Bank. By December the young stages had disappeared at our sampling level and were not recorded again until July, 1939, when they began to appear in the extreme north-west as in August, 1938.

The young of Nyctiphanes were never found in such concentrations as to indicate a definite spawning area, unlike the other species described, nor were spermatophores found. Since their adults were similarly scarce, however, there is no particular evidence to suggest that they do not breed in our area. Einarsson (1945) found them spawning in the Skagerrak, and concluded that they are now indigenous to the North Sea, while Ruud (1928) recorded furcilia and cyrtopia stages off the Norwegian coast near Möre, but noted that this species " is not found to be adult or spawning in our waters." Künne (1937) also found young stages of Nyctiphanes in the Dover Straits area presumably derived from the breeding areas in the Channel. Perhaps the best evidence for their breeding within the North Sea is provided by the widespread and frequent association of adults and young, with the implied general tolerance of North Sea conditions.

Nematoscelis megalops G. O. Sars. (Plates XCIV–XCVII.)

There were only two records for this species, one in February, 1938 and the other in February, 1939. On both occasions it was found off the Aberdeenshire coast.

Thysanöessa inermis (Krøyer). (Plates XCVIII–C.)

Our survey showed this species to be particularly characteristic of Scottish waters, where it occurred either in the adult or larval phase during every month.

In the Skagerrak region and off the Norwegian coast the adults occurred less frequently, while over the central North Sea they were rarer still. Latitude 55°N. marked the southern limit of the distributions.

In 1938 the larvae were found in the north-western area (most abundantly close to the Shetlands) from May until August, the latter month yielding a mixed population of larvae and adolescents. Elsewhere they were found in fair numbers over the Great Fisher Bank and in the mouth of the Skagerrak in June and July. In 1939 the larvae were entirely confined to the north-western area. They began to appear in April[1] and reached maximum values in May, when they were most densely aggregated off the Moray Firth. From June until the end of the survey in August the numbers steadily declined, and by August of both years the larvae were entirely absent from the records in southern Scottish waters.

Lebour (1926) considered that " adults occur in the spring, when they are breeding, larvae occurring through the summer and disappearing." Einarsson's observations (1945) agreed with this, and ours also do. Therefore, the regular appearance of these larval swarms in the Orkney–Shetland region and off the

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[1] On the Iceland line. Lucas, Marshall and Rees (1942) found a dense swarm of the larvae west of the Orkneys in March, 1939.

Moray Firth suggests that we might now add these areas to the list of spawning places summarized by Einarsson. This is confirmed by the observations in March–May, 1938, of females with spermatophores from Orkney to the Firth of Forth. The concentration of larvel *T. inermis* in the Skagerrak area in 1938 agrees with Einarsson's chart summarizing the data on breeding areas, and showing an extensive spawning belt off the Norwegian coast from the Skagerrak northwards.

Thysanöessa raschii (M. Sars). (Plates XCVIII–C.)

The waters off the Norwegian coast and around the Skagerrak contained the bulk of the stocks of this species. Dense swarms of adults were taken in the latter area in July of both years. In the north-west it was fairly common except during the summer, but it was rarer over the central North Sea. Latitude 55° N. marked its most southerly point of occurrence.

In 1938 the young stages appeared on the eastern half of the Pentland Firth–Bergen line in June and July, but mainly in the former month. In 1939 far denser broods were taken in the western Norwegian waters in May and in the mouth of the Skagerrak from May to July, as also applied to several other species. In particular, females were taken with spermatophores from April to May. Adolescents began to appear in July, but by August both larvae and adolescents were absent.

T. raschii had quite a similar distribution to that of Meganyctiphanes, and 1939 was apparently the better brood year for both euphausians. Einarsson (1945) lists *T. raschii* as breeding in East Icelandic and West Greenland waters, while Macdonald's work (1928) showed it to have two spawning periods in Loch Fyne. Our findings suggest that it may also breed in the waters off the Skagerrak, and probably, further north off the Norwegian coast.

Lamellibranch larvae. (Plate CI.)

The main productive period in 1938 extended from May to July, the most important areas lying to the north-west (particularly in the Orkney–Shetland region) and in a region extending over the Dogger Bank (especially the north-east end) and the Great Fisher Bank. We have already drawn attention to the Dogger production in the earlier 1932–37 survey (Henderson and Marshall, 1944). The larvae in 1938 were concentrated in quite sharply delineated patches, those over the two banks persisting from May to July, while the north-western population was mainly evident from June to August.

In 1939 the production of larvae was again not considerable until May, when the beginnings of the populations in the main areas could be seen. Over the bank areas the patches became densest in June and July; in the north-west the peak period of production was reached in July.

The relationship between the larval patches and the bottom fauna and the possible effect of currents on their distribution is discussed in a later section (p. 207).

Cladocera. (Plates CII and CIII.)

It was not possible to separate the species of Podon and Evadne in this material, and the value of the data is consequently reduced. Both showed a very patchy distribution in time and space.

In both years the peak period for the swarms of Evadne (Plate CIII) extended from May to July. The densest populations were found in the north-western area and around and within the Heligoland Bight and the mouth of the Skagerrak. The relative permanence of the north-western stock contrasted with conditions over the remainder of the North Sea, where the patches tended to come and go quite rapidly.

Podon (Plate CII) was rarely taken in such high numbers as Evadne, but in general there appeared to be some degree of correlation between the distribution of the two genera. In the north-western area it was quite sparse until July in both years; it provided fairly dense swarms in the central North Sea in August, 1939, when Evadne was very scarce.

Amphipoda. (Plates CIV–CV.)

Only the three most commonly occurring species have been considered, *i.e.* the hyperiid, *Themisto abyssorum*,[1] the gammarid, *Apherusa clevei*, and the caprellid, *Phthisica acaudata*. Among other less common hyperiids which were recorded were *T. compressa f. bispinosa* and *Hyperia galba*, while among the gammarids, *Metopa alderi* and *Bathyporeia pelagica* were not uncommon.

Themisto abyssorum (Boeck).[1]

Since this species was never taken in numbers greater than 10 per block the scale of symbols used for the other two amphipods was not adopted. Each black square on the charts merely indicates its presence.

During the two years the distribution conformed to a sequence of well-defined changes in area and time. Following a wide distribution in the early months of 1938 (when it was particularly widespread except in the extreme north-west and the south-east), it occurred much less frequently during the spring and early summer, mainly in the central waters. In August it suddenly increased in the extreme north-west, and from this region it apparently spread eastwards and southwards until the end of the year, culminating in a wide distribution. It was noticeably absent from the Heligoland Bight, however, where in fact it was only recorded once during this survey. Events in 1939 followed a quite similar pattern. It was almost entirely restricted to the Dogger Bank in April and May, and it reappeared in the Orkney–Shetland area in July and August.

[1] This amphipod was identified during this survey as *T. abyssorum* (Boeck), and is presumably the same form as was found by Künne (1937). We now have reason to believe that most if not all may have been *T. gracilipes* Norman.

Apherusa clevei G. O. Sars.

This species rarely extended north of the line running from the Forth to the Skagerrak; south of this it had a wide distribution in later summer, autumn and winter.

The denser swarms were generally sharply defined, and associated with definite areas during the twenty months of the survey. Particularly was this so just off the Humber in February and March, and from July to December (except September) in 1938, and in August, 1939. South of the Bremen route this amphipod was never taken in any abundance.

As far as the two years can be compared it is clear that in 1939 this species was both less abundant and frequent in our records.

Phthisica acaudata (Gronovius).

This caprellid was mainly found in the Southern and Heligoland Bights and around and within the mouth of the Skagerrak. Only once was it found outside these areas during our survey, this being in November, 1938, when it occurred off the Forth. In general it was widely distributed and most numerous over these southern and eastern areas in the autumn and winter, while in the spring and part of the summer it was only present in the extreme Southern Bight.

Starting from the latter restricted distribution an orderly succession of changes gave rise to the winter population in 1938. From May to September the area of distribution progressively expanded in a north-easterly direction, until in October it appeared in fair numbers off the North Jutland coast and in the mouth of the Skagerrak. From March to August in 1939 there were signs of a recurrence of this cycle.

Similar changes were noted in the earlier report on the southern North Sea survey (Henderson and Marshall, 1944). Since the beginning of the recorder surveys in 1932 this sequence has in fact been evident in six years out of eight, although at times it was commoner off the Humber than in 1938–39.

Cyphonautes larvae. (Plate CV.)

Only the results for the more northern lines have been plotted, as these covered the main productive areas.

The north-western area was by far the most important, the entrance to the Skagerrak being the only other region where the larvae were found in any quantity. In both years a marked increase in numbers took place in the Orkney–Shetland area in May, followed in June by an intensification of this production, which by July and August had spread to the more southerly Scottish waters.

The great difference in production between the northern and southern North Sea is interesting. Savage (1926) found these larvae to be far more abundant in July, 1922 in the Shields area than in his more southerly stations off the Yorkshire and East Anglian coasts. Possibly the structure of the littoral zone is an important factor, *e.g.* the rockier coasts of Scotland may well provide a greater number of suitable sites for the fixed life of the adult Polyzoa. Hincks (1880) lists 134 species of Polyzoa (Ectoprocta) from the Shetlands as against 87 from Northumberland and Durham.

Decapod larvae. (Plate CVI.)

The charts show that larval production reached its peak in July and August, and that by far the densest concentrations were found in the Southern and Heligoland Bights. Over the Dogger Bank and in Scottish coastal waters smaller numbers were taken, while only in July, 1939, was a substantial population to be seen in the mouth of the Skagerrak. In comparison with these areas the central area north of the Forth–Hamburg route was quite barren. It was just in this area, however, that we found dense patches of Lamellibranch larvae. In both years decapod larvae became more frequent in the April catches, but not until May were major increases recorded. In contrast with other larval forms was the not infrequent presence of decapod larvae in the winter records, on which we have already commented in relation to the earlier survey (Henderson and Marshall, 1944).

The average monthly catches plotted in Text-figs. 2 and 3 show that " larval production " on the Bremen and Rotterdam routes was much greater in 1938 than in 1939, a comparison of these figures with those shown in ' Bulletin ' No. 6 further showing that the averages for July and August on the R and B lines respectively were maximal for the entire period. These histograms also show that the populations reached their peak a month earlier on the more southerly Rotterdam route ; similarly at the north-eastern end of the Hull–Copenhagen line the catches were poor until August in both years, whereas on the south-western section high numbers appeared in July (*cf.* Echinoderm Larvae).

Stomatopod larvae.

In August, 1938, a few Alima larvae were taken on the southern end of the London–Esbjerg route, off the East Anglian coast. Our earlier survey (' Bulletin ' No. 6) showed them to have been present in much the same position in August, 1937, September, 1935, and from August to October in 1934.

One of the 1938 specimens has been identified as a larva of *Squilla desmarestii*, which Russell (1927) found in the Plymouth area in July and August, 1925. Whether this should be an annual feature of English Channel plankton or not, the appearance of the larvae in the Southern North Sea later in the year may be of significance as an indication of Channel water.

Echinoderm larvae. (Plate CVII.)

In both years by far the greatest production took place from May to August in the Southern Bight, the Heligoland Bight and off the Skagerrak (*cf.* 1932–37, Henderson and Marshall, 1944). In north-western waters much smaller populations were produced rather later in the year, these appearing in August and September in 1938 and in July and August in 1939. A difference between the two years was found in the absence of a Humber patch in 1939.

In 1938, as the season advanced, the main larval swarms were produced in a regular south to north sequence (again, generally, as in 1932–37), although in 1939 this was not quite so clearly marked. Fair numbers of larvae first appeared in the two Bights in May, followed by an intensification of this production to a maximum in June, when a well-defined patch also appeared off the North Jutland coast. By July the numbers in the Southern Bight had markedly decreased, but the Heligoland Bight broods, even if less numerous, were still abundant, while the North Jutland patch had become denser near to the coast. Finally, in August (apart from one rather northerly patch) the larval population in the Heligoland Bight had decreased considerably, but further north a dense patch had now appeared in the mouth of the Skagerrak while the North Jutland concentration had decreased a little. A later section (pp. 206–210) discusses the probable relationship between this succession in area and time and the effect of hydrographical conditions on the reproductive activities of the bottom living adults, and also attempts to trace the correspondences between the distribution of the latter and the planktonic larvae.

Oikopleura spp. (Plate CVIII.)

The main months of abundance for *Oikopleura spp.* extended from April to September. In 1938 signs of an increase in the population were first apparent in the Southern Bight and over the Dogger Bank in April and May ; in the north-west there were two main periods of abundance in June and August. By contrast, the indications of an increase in 1939 were already obvious in both the north-western area and the Southern Bight in February, this being followed by the development of the former population to a maximum in May. In the Southern North Sea it was not until June that high numbers were recorded.

The average monthly catches set out in Text-figs. 1–3, following on from those published in ‘ Bulletin ’ No. 6, show that on the Hull–Bremen and Hull–Rotterdam lines maximum numbers were reached in 1938. Savage (1937) has shown how important Oikopleura spp. can be in the diet of herrings, especially in the northern North Sea, and these fluctuations in area and time are probably of considerable importance in the economy of the sea.

Tomopteris.

At certain times *Tomopteris* have been numerous in the records, although they were generally scarce during these two years and have not been illustrated. The greatest numbers were found over and to the north of the Dogger Bank from August to October in 1938, whilst there were moderate numbers in the north-west in August, 1939.

Planktonic Indicator Species.

The pioneer work of Russell (*e.g.* his summary, 1939) on planktonic indicators has clearly shown that, provided a good all-round knowledge of these organisms is available, they can be used within varying limits to typify certain water masses. Fraser (1937 and 1939) and Künne (1935) have shown some of the zooplankton groupings which may be expected, and a more detailed pattern of distribution of indicator forms at 10 metres depth is now revealed by this survey. Rae and Rees (1947) have already shown such a pattern for the Copepoda, and have drawn attention to some of the parallels between these and the other zooplankton organisms.

Unfortunately there is far too little information on the breeding of indicator species in the North Sea, so that for some species the balance between the actual dispersal of organisms by water movement and the apparent movements which may be caused by a sequence of breeding in two or more centres is difficult to assess, although it will be considered. A further factor which must be considered at all times is that of vertical distribution, since the recorder collects samples at a constant depth of 10 metres.

Provided such limitations are recognized, this survey with its regular monthly records permits us to follow changes in distribution quite closely. At the same time, knowledge of the monthly fluctuations in numbers shows at what times of the year the various organisms are most numerous and therefore become most useful as indicators. For example, Tait's work (1937) has shown that the strength of the northern inflow may often reach a maximum during the early months of the year, a time when the stocks of indicator organisms such as *Sagitta elegans* and *Limacina retroversa* are very low while *Clione limacina* may be entirely absent from our northern records. Taking this to its logical conclusion, negative results (as Farran, 1933, has pointed out) do not necessarily mean the absence of the water type with which the indicator is associated. On the other hand, the northern influence tends to extend later and further, the more intensive it is, and by continuous sampling over a wide area the changing boundaries between organisms and the extent of their distribution when present at 10 metres can be fairly accurately found. This not only reveals the basic similarity between the distributions of the indicators of a particular water mass, but also the differences between them, which are no less important. The reader is referred for example to Text-figs. 4 and 5, where the spatial relationships between the distributions of *Sagitta spp.*, pteropods and euphausians are summarized for some of the more significant months ; the distributions of associated organisms can be seen in the plates, and they can be compared with the results obtained by Rae and Rees (1947, figs. 3–8 and plates). Such differences and some suggested reasons to account for them will be discussed, but inevitably some of these are bound up with vertical distribution and behaviour, on which there is as yet little information from the North Sea.

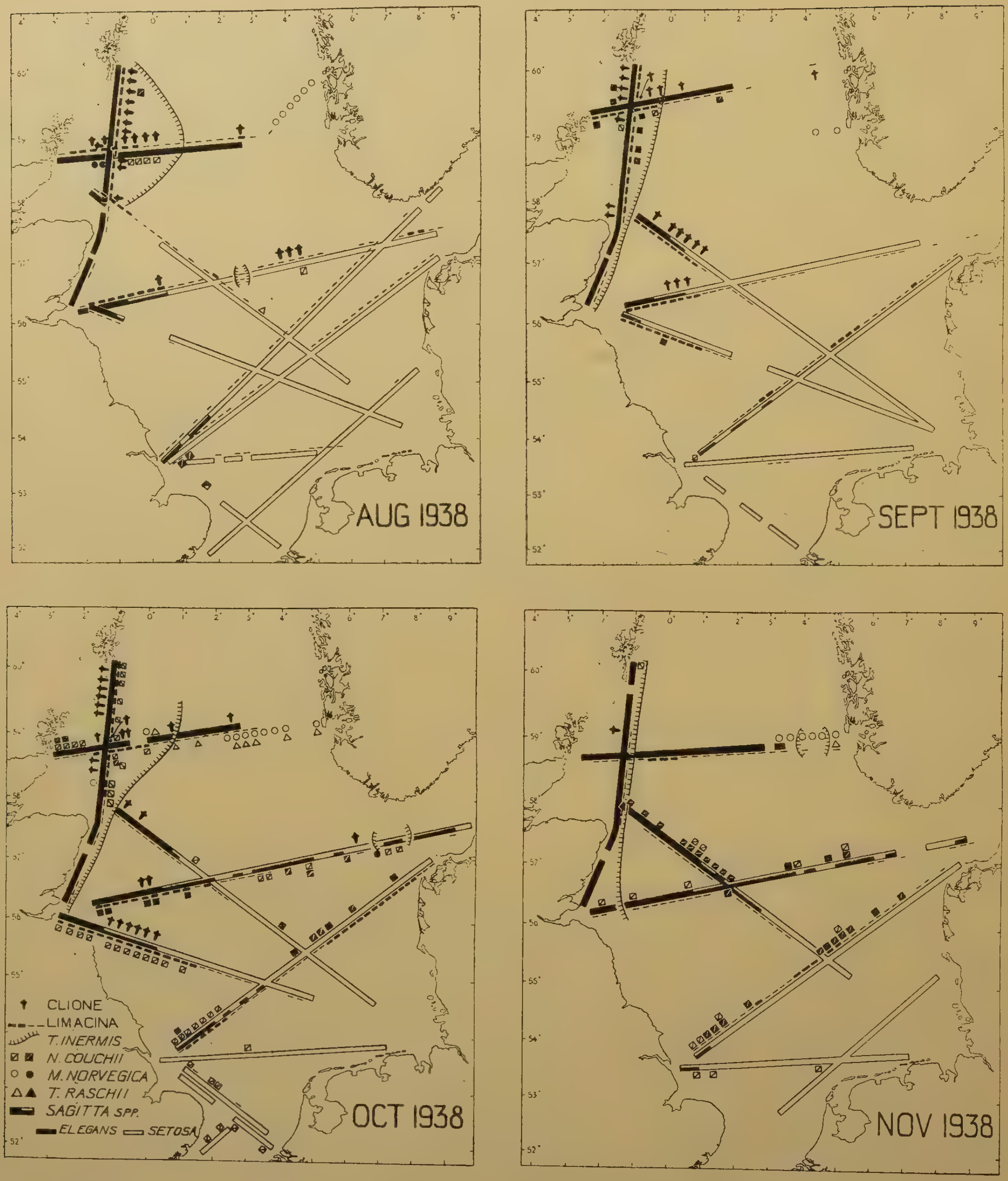
Taking the 1938–39 period as a whole, it is useful first to consider the organisms under regional headings; for this purpose the north-western, north-eastern, central and southern regions have been taken. Varying numbers of species are recorded for each, but certain groups of them are seen to be more typical of one region than the others. These undoubtedly "indicate" water masses which come under different influences and so vary in area and inter-relationship.

The North-western Region.

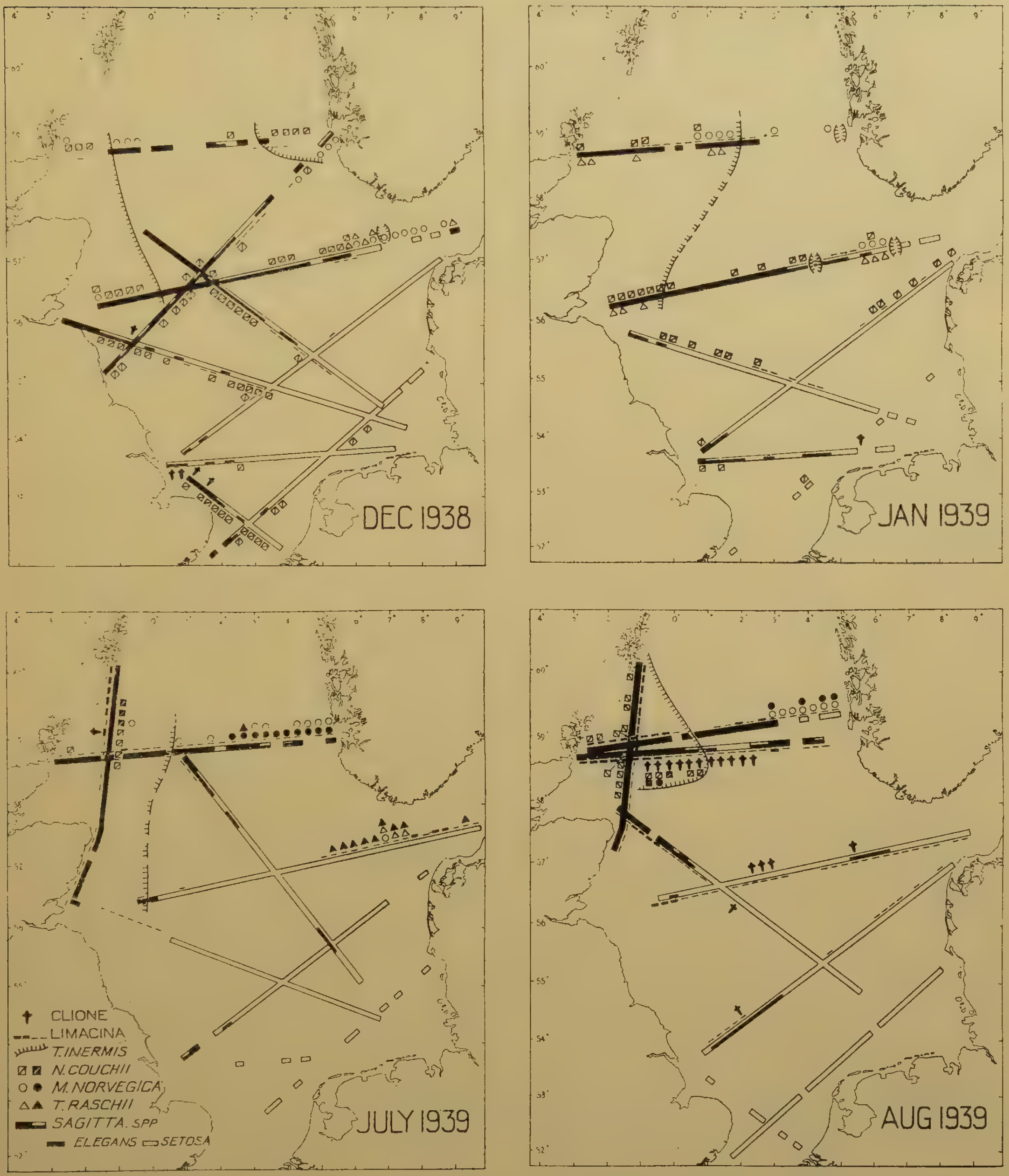
Sagitta elegans and the euphausian *Thysanöessa inermis* were the most typical organisms in that the bulk of their populations at 10 metres were contained within this area, which forms the main if not the only North Sea breeding area for both types. *Limacina retroversa* was more widely distributed, but nevertheless can be included here since the greater part of the North Sea stocks were found within the "*elegans*" water. *Clione limacina* was commoner in the north-west than elsewhere in the northern North Sea, and it is possible to trace its southerly spread both within and away from the area. *Nyctiphanes couchii* and *Themisto abyssorum* are also considered under this heading, although both are less typical than all the foregoing species, but are none the less usually commoner in this region than in other parts of the North Sea, and probably spread into neighbouring areas from the north-west. Other forms, such as the Cladocera and Oikopleura, which are found in this region and elsewhere, have not been identified precisely enough to determine any natural limitations. Finally *Sagitta serratodentata* and *Nematoscelis megalops*, which were found only in this area, come under the category of visitors. The region is roughly that indicated by the copepods *Metridia lucens* and *Candacia armata* (Rae and Rees, 1947).

Sagitta elegans Verrill.

Meek (1928), Wimpenny (1937), and Fraser (1939) have shown that during years of considerable northern influence *Sagitta elegans* breeds in the north-western mixed coastal and oceanic waters off the Scottish and north-eastern English coasts, and in no other part of the North Sea has it yet been observed to reproduce. This survey adds some definition to Fraser's (1937) illustration of the relationship between *S. elegans* and *S. setosa*, the indigenous form in the North Sea basin. Not only may "*elegans*" water displace "*setosa*" water in any one year as in 1938 but, at this level of 10 metres, there may be considerable mixture between the two. The summary of hydrographical information for 1938 contained in the Annual Report of the Fishery Board for Scotland (1939) states that the northern inflow "apparently renewed itself for a third time in September, after which there was unmistakable evidence of a considerable recession of the Atlantic influence from the Northern North Sea." The reciprocal movements of the two Sagitta complexes from September onwards may have been initiated by this increase in pressure


AUG 1938
SEPT 1938
OCT 1938
NOV 1938
CLIONE
LIMACINA
T. INERMIS
N. COUCHII
M. NORVEGICA
T. RASCHII
SAGITTA SPP.
ELEGANS
SETOSA

TEXT-FIG. 4.—Charts showing diagrammatically the associated distributions over the North Sea of Clione, Limacina, four species of euphausians, and two species of Sagitta from August, 1938, to November, 1938. The larger quantities of Limacina are denoted by the thicker broken line, and smaller quantities by the thinner one. For other details, and distributions of other forms, see Plates LXXXIX to CVIII.


DEC 1938
JAN 1939
CLIONE
LIMACINA
T.INERMIS
N.COUCHII
M.NORVEGICA
T.RASCHII
SAGITTA. SPP
ELEGANS
SETOSA
JULY 1939
AUG 1939

TEXT-FIG. 5.—Continuing Text-fig. 6, for December, 1938, and January, July and August, 1939 (see legend to Text-fig. 6, and identification key on the July chart).

from the north, but what is more important is the relationship between this influence and that from the south.

The " see-saw " or " buffer " relationship between the northern and southern waters containing the two forms respectively would appear to be an important factor, as Russell (1935) has earlier suggested. While the bulk of the *elegans* and *setosa* populations remained quite separate during the summer months, reference has already been made to the increased degree of mixing which accompanied them during the autumn and winter. The easterly spread of sparse populations of *S. elegans* into the "*setosa*" area, which was most marked along the Forth-Skagerrak line, may simply reflect the overlap between the surface waters containing *S. setosa* and the underlying waters where *S. elegans* is dominant, to which possibility Fraser (1939) has already directed attention. Furnestin (1938), in a section across the north-western North Sea (the Fladen area) during September, 1936, found *S. elegans* to be the dominant form in the more saline bottom layers. At depths of 20 metres, which most nearly correspond with our data, his eastern stations from longitude 1°–2°E. consisted of a dominant *setosa* population mixed with a few *elegans*. His catches from two more western stations, situated at about the Greenwich meridian and east of stations yielding a pure *elegans* population, contained higher percentages of *S. elegans* than the first ones. Such a succession from east to west is very similar to our results on the Forth–Copenhagen line, and quite possibly there are two effects to be considered. The expansion of "*elegans*" water shown by our samples at 10 metres may have been part of a more general movement also involving an extension of the bottom layers of this water underneath the "*setosa*" water, the appearance of *elegans* in the "*setosa*" layer being, as it were, a surface reflection of these deeper-seated movements perhaps associated with the withdrawal of Baltic water. In association there might also be vertical migration and increasing vertical water movements, the latter being known to be more extensive during the colder periods of the year. The distributions of *Nyctiphanes couchii* and *Themisto abyssorum*, together with certain copepods (Rae and Rees, 1947), as well as other organisms, showed similar changes from September to October in 1938. Such similarities perhaps rather suggest water movements than vertical migration. None the less these results may be summarized by concluding that the relatively sharp ecological boundaries revealed at 10 metres during a series of months and the subsequent mixing, together with the annual variations of such distributions, all seem to have prospective value as direct indications of hydrological changes in this area of significance for the fisheries.

The distribution of *S. elegans* in the Southern North Sea agrees very well with the general ideas on the circulation in this area (*e.g.* Carruthers, 1925). It would seem to have moved, together with Clione, southwards down the East Anglian coast in December, 1938, and eastwards towards the continental coasts during the early months of 1939, as did the appropriate copepod indicators. This agrees with Künne (1937) closely, since he found during the winter that *elegans* could extend as far south as the Thames estuary and eastwards into the Heligoland Bight, but was most abundant in the Flamborough–S.W. Dogger region. Our observations have shown that this off Humber area contained an almost permanent stock of *S. elegans*, and we have to consider whether this might be an isolated stock. Although Wimpenny (1937) also found *elegans* usually present, the associated presence of more typical Dogger Bank organisms, together with the successive arrival there of other and scarcer north-western ones, suggests that a seasonal recruitment may also occur and that from it the more widely dispersed individuals probably originate. It is much less likely (see Russell's generalized picture of Sagitta distributions, 1939) that there is any regular entry of *S. elegans* into the North Sea from the Channel, although not impossible in certain years.

Limacina retroversa Fleming.

The well-marked development of Limacina in the north-west during the summer was most intensive within the coastal regions of "*elegans* water" off Orkney and Shetland, whereas off the Forth the denser concentrations extended well to the east of the "*elegans-setosa*" boundary. A marked coastal development was also found west of Orkney on the Iceland line in 1939, where Lucas, Marshall and Rees (1942) showed that it began in April, and by June had given rise to a dense mass of small and growing stages mixed with adults. Like *S. elegans*, the pteropod was most abundant in the Orkney–Shetland region in July, 1938, but did not attain comparable densities in the more southerly Scottish waters until August and September. How far the latter is due to actual invasion from the north as opposed to local development it is not easy to decide on our present data. To some extent successive local breedings may occur, but the associated spread of so many different organisms over a long period (*cf.* Rae and Rees, 1947; Lucas, 1941 and 1942; Stubbings and Henderson in the press) strongly favour the existence of considerable southerly and easterly movements.

Outside the north-western area Limacina was found in small quantities, particularly in 1938, when it was most numerous over the Great Fisher Bank and off the entrance to the Skagerrak. It was associated with young *Thysanöessa inermis* in the Skagerrak in June, but in general, outside the north-western area, these two species, whilst often adjacent, appear to have been almost mutually exclusive. On the other hand, Clione was seldom found unaccompanied by Limacina in these northern waters (*e.g.* July–August, 1938 and August, 1939) although this was not so in the south.

The hydrographical summary given in the Annual Report of the Fishery Board for Scotland in 1938 (1939) states that in the latter half of June the drift bottle data gave good evidence "of a renewed thrust southwards of the Atlantic incursion from the north," and it was during this month that "large numbers of bottles were found on the North Sea Norwegian coast." The marked easterly component of this drift might possibly account for the dispersal of Limacina, etc., to the Fisher Bank region and even further. The

1939 data from June to August provides a contrast in that our records of *T. inermis* larvae were restricted to the north-west, although a local population of Limacina (with Clione in August) was found in and off the mouth of the Skagerrak, and over the Fisher Bank.

A consideration of the above data makes a northern origin of the Fisher Bank populations of Limacina and young Clione more probable than an origin from the Skagerrak. Moreover the writer can find no evidence from published work that Clione breeds in the Skagerrak. Yet, the possibility of an intimate biological relationship between the Skagerrak and outside waters is recognized by many workers. Practically all the plankton elements which Fraser (1937, 1939) has listed as characteristic of cold, warm and mixed coastal and oceanic water in the north have also been found in the Skagerrak. Of the mixed water indicators, *Aglantha digitale* (Kramp, 1927) and probably *S. elegans* and Limacina breed within the Skagerrak, while also at home and often breeding there are the four common euphausian species described in this paper. The more saline bottom waters which flow into the Skagerrak from the Northern North Sea must at times establish a hydrographical continuity between the two areas which may also become a biological continuity. Rae and Rees (1947) discussed this in dealing with the distribution of the copepods, and came to the conclusion that such continuity may be inferred from our recorder data. They also mentioned the possible importance of the Skagerrak as the centre of a rich population which, although recruited from outside, might nevertheless in its turn invade the neighbouring parts of the North Sea. All the available evidence suggests that the forms which would be the most useful indicators of such an invasion have their habitat in the deeper layers of the Skagerrak, *e.g.* Kramp (1927) most often found the Hydromedusae, which are indicative of mixed coastal and oceanic water in the north-western area in the intermediate or bottom layers of the Skagerrak. Whether such organisms could live successfully in the low salinity water forming the Baltic effluent is uncertain. None the less they could also be carried into the North Sea in the deeper and more saline outgoing currents from the Skagerrak such as Eggvin (1940) has shown in a hydrographical section from the Orkneys to Jaerens rev.

Another contrast between Limacina and *S. elegans* is provided by the development of a dense patch of the former off the North Jutland coast in October, 1938. This seems likely but not certainly to have originated by local reproduction, and it was accompanied only by *S. setosa*. There is no doubt, however, that the bulk of the Limacina population of the North Sea was produced in the north-western waters from which thriving swarms were carried southwards along with *Sagitta elegans, Clione,* and other forms to the southern North Sea.

Clione limacina Phipps.

The origin of the young Clione which appear in the northern North Sea during the summer does not appear to be clearly known, although Hjort and Ruud (1929) found that Clione breeds in both arctic and Atlantic regions. Lucas, Marshall and Rees (1942) recorded a number of young stages mainly on the western end of the Pentland Firth–Iceland line from March to May in 1939. If, as seems likely, Clione does not breed within the North Sea, then the young stages which enter from the north (having perhaps a mixed origin) should give a particularly reliable indication of water movement.

While Clione was definitely associated with Limacina, it is interesting to note that during its undoubted southerly spread it only attained its maximum on the lines sampling the Scottish area south of the Moray Firth *after* the Limacina populations had attained their maximum. Thus on the Pentland–Hamburg and the Forth–Skagerrak lines this maximum was reached in August, while the records for Clione were most numerous in September. Similarly on the southernmost Leith–Hamburg route the peak month for Limacina was September, while Clione was commonest in October. This is perhaps reflected in the apparent failure of Limacina to accompany the southern Clione mentioned above. Again, even when Clione accompanied Limacina in the north-west it was often well to the east of the Limacina concentrations.

The relationship of Clione to the *S. elegans* complex (Text-figs. 4 and 5) may be summarized by noting that there were 77 records of it within "*elegans*" water as against 29 records outside this water. An analysis of the latter figure shows, however, that it was found close to the boundary between *S. elegans* and *S. setosa* 12 times, and that 11 of these 12 records fall in September and October, 1938, when it was spreading into southern Scottish waters. Another 9 of these records are from the Fisher Bank area in July and August, 1938, and probably resulted from the drift away from the north previously discussed in the section on Limacina; on all these 9 records it was associated with a pure *S. setosa* population.

After the gradual extension in Scottish waters from August to October in 1938 it would seem that this southerly movement persisted, since Clione was found off the Humber (together with *S. elegans*) in December. In the earlier survey described in 'Bulletin' No. 6 Clione was found on the Hull–Copenhagen line in January, 1935, and in January and February, 1936. All these individuals presumably drifted to these areas from the north, for we have as yet no evidence of an entry from the Channel. They correspond in general with the arrival in similar places of the north-western copepods (Rae and Rees, 1947). Künne (1937) also found young Clione during the winter in the southern North Sea and described it as being common in the north-western part, but also recorded it southwards as far as Yarmouth and eastwards to the Austern Grund. Moreover his results from October, 1934 to January 1935, show that Clione was restricted to the S.W. Dogger Bank–Flamborough area in the former month and did not attain the above wider distribution until the latter month, thus lending further support to our observation (p. 194) that during the winter Clione in company with *S. elegans* may drift eastwards across the Southern Bight.

Thysanöessa inermis (Krøyer).

We have shown this euphausian to have its centre of abundance in Scottish waters, where in both years we found numerous young stages. In June and July, 1938, we found it abundant in and off the Skagerrak, but in 1939 it was restricted to the north-west and, whether in the larval or adult phase, it was never found much further south than the latitude of the Forth.

This restricted distribution is best shown by comparing the summer distribution of *T. inermis* with *Nyctiphanes couchii* during 1938. In June and July the north-western waters were entirely populated with the larvae of the former, but no adults of either species were found. In August (Text-fig. 5), when larval and adult Nyctiphanes began to appear in the Orkney–Shetland region together with the mixture of adolescent and larval *T. inermis*, the young stages of the latter had disappeared from our sampling level in the southernmost Scottish waters. By September only adult *T. inermis* were to be found, almost restricted to the Moray Firth, while further south a few Nyctiphanes larvae had appeared off the Forth. The October records, which revealed such a striking increase in the distribution of Nyctiphanes to the east and south, showed that *T. inermis* was still restricted to the Scottish area.

It is evident that we are dealing with two organisms having very different patterns of behaviour and biological requirements. *S. elegans*, which like *T. inermis* breeds and has its centre of distribution in the north-west, also spread away from this area, particularly to the east, and possible mechanisms for this drift have been discussed (p. 191). We have, in fact, organisms such as Nyctiphanes, *S. elegans*, Limacina and Clione on the one hand, which appear to be dispersed away from the north-west in mass. On the other hand, adult *Thysanöessa inermis* (a typical member of this north-west community) and *T. raschii* and *Meganyctiphanes norvegica* (which presumably enter this area with the northern inflow) do not appear to spread in this way ; only occasional specimens have been found in the southern North Sea (Künne, 1937), and we found none during our survey.

Until we have more data on the seasonal changes in vertical behaviour we must be limited in trying to interpret the changes we observe in the horizontal plane. It would be interesting, for example, to know what proportion of euphausian life is spent on the bottom and how this varies with the season. Most of the evidence indicates that this is very considerable for adults at least. At all events these euphausians with their marked vertical movements make less satisfactory biological "drift bottles" than the less active members of the north-western community of organisms.

Nyctiphanes couchii (Bell) and *Themisto abyssorum*[1] Boeck.

The changing patterns of the distribution of these forms followed such broadly similar trends that they are best considered together. Briefly both organisms had a wide distribution during the autumn and winter, but became restricted in area during spring and summer, Themisto in particular being mainly confined to the middle latitudes and the Dogger Bank. In August, 1938, however, both organisms appeared quite suddenly in the Orkney–Shetland area, and by October became widespread eastwards to the Skagerrak and southwards to the Dogger Bank. (Nyctiphanes was also fairly common off the East Anglian coast.) In July and August, 1939, they again entered the north-western area together, as if about to repeat the cycle seen in 1938.

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[1] See footnote on p. 186.

This evidence suggests that a residual stock of these two organisms populated the North Sea during the spring and early summer, and that a replenishment of these stocks, which give rise to the widespread distributions in winter, was at any rate partly effected by the arrival of the two forms in the more northern Scottish waters and their apparent dispersal eastwards and southwards. We have already remarked on the easterly infiltration of small numbers of *S. elegans* into " setosa " waters which, like the rapid spread of these two organisms, took place during October, 1938. This apparent movement may, like that of *S. elegans*, be explained by their appearance in these upper water layers by vertical migration, or by vertical movement of water from the underlying waters of higher salinity. A rather similar change occurred in the case of *Centropages typicus* (Rae and Rees, 1947), and there are some other resemblances between its distribution and that of the two animals discussed here.

Einarsson (1945), in summarizing the information on the distribution of Nyctiphanes in the North Sea, very arbitrarily asserts that Mielck and Künne were unlikely to be right in using Nyctiphanes as an indicator of northern water. He further suggests that the North Sea has become populated (since the time of the investigations by the International Council) by invasion from the English Channel, and draws a parallel between the increasing distribution of this euphausian and *Biddulphia sinensis* during these years. Künne (1937) has evidence to suggest that both Nyctiphanes and *T. abyssorum* may enter the Southern North Sea from the channel but, finding both organisms to have a centre of abundance in the Flamborough–S.W. Dogger Bank region, he concludes that recruitment from the north is the more important. It would be easier to form a more comprehensive valuation of these organisms as indicators if more knowledge was available of the breeding areas. Although this survey has provided some presumptive evidence for Nyctiphanes breeding in the North Sea, it should be noted that the majority of the larvae recorded were advanced cyrtopia stages. Furthermore there is yet no definite evidence of *T. abyssorum* (see footnote on p. 186) reproducing within the area. It is, however, certain that both forms can lead a successful vegetative existence for considerable periods in the North Sea under varying conditions; Künne (1937), for example, found Nyctiphanes extending right into the Heligoland Bight as far as the river mouths. The origin of the mixed stock of larval and adult Nyctiphanes which appeared in the Orkney–Shetland region in the summer of 1938 and 1939 is rather obscure and the Iceland line during 1939 gave no clue to this problem. On the other hand, our records for 1946 show adult Nyctiphanes to have been present in September just north of the Hebrides, while in November a sparse population of late cyrtopia and adolescents was recorded west of the Shetlands, which may indicate breeding areas off the west British coasts.[1] The possibility of a double origin thus makes their use as indicators less straightforward than the more typical north-western forms, *Sagitta elegans*, Limacina and Clione. An added complication is their powers of apparently successful vegetative existence as a residual population of relatively shallow waters during the spring and summer ; in the case of Nyctiphanes, this may partly explain its difference in distribution and migration from the other euphausians.

Sagitta serratodentata Krohn.

This was the only representative of the community listed by Fraser (1937, 1939) as typical of warm oceanic water which was found at the recorder sampling level. It appeared off the Orkneys in April and May, 1939, a time when the northern inflow may be expected to have reached a maximum speed (Tait, 1937).

Nematoscelis megalops G. O. Sars.

This euphausian, which Einarsson (1945) has described as a " southern guest " in North Atlantic waters, may be tentatively added as an indicator of warm oceanic water entering from the north-west, although the time of its recording, in February of both years, and its position as far south as the region of the Aberdeenshire coast, are both rather surprising.

The Central Region.

Sagitta setosa J. Müller.

This is the characteristic and indigenous form of this region. It was most abundant in the more central areas between 57° and 54° N. latitude, and common but less abundant in the Southern and Heligoland Bights. The gammarid *Apherusa clevei* was often associated with it and likewise less abundant in the two Bights. Rae and Rees (1947) found the copepods *Labidocera wollastoni* and *Isias clavipes* " apparently indigenous to the central North Sea," and suggested that they should be added to *S. setosa* as typical residents. Wimpenny (1946) and Lucas (1941 and 1948) also show that over a number of years these waters were populated by a larger form of *Rhizosolenia styliformis* than those to the north-west. Whilst there are likely to be other typical species or varieties (*e.g.* perhaps certain species of Cladocera), this group of five associates amply confirms the distinction made earlier by Russell (*e.g.* 1939) between the true North Sea waters and those to the north-west. Rarely, or only in small numbers, are they to be found associated with the forms considered to indicate the other waters.

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[1] Frost (1932) has shown Nyctiphanes to breed off the south coast of Ireland. Nyctiphanes may well have increased its area of distribution northwards off the west coasts of the British Isles in parallel to that suggested by Einarsson for the North Sea.

On p. 179 reference was made to the occasional appearance of *S. setosa* in the water on the Norwegian side of the Northern North Sea, which may provide evidence for northerly water movements (*cf.* Fraser, 1939, Chart II). Lucas (1948) has referred to the south-eastern population of large-celled *Rhizosolenia styliformis* spreading northwards to Norwegian coastal waters during the autumn of 1938, and his data for October showed the presence of a small population of such large cells off Bergen. Whilst it was not until December that *S. setosa* was found in this latitude, this could well have resulted from the persistence of this movement. The few specimens of *setosa* which were recorded close to the Norwegian coast from March to June in 1939 may perhaps have been carried there in association with the Baltic outflow, and in July and August there was unmistakable evidence of a mass extension of this form northward along the outer edge of the *elegans* population. Similarly, a patch of *Anomalocera patersoni*, which had previously only been recorded further south, appeared in almost exactly the same area, although this comparison cannot be given much weight in view of our sampling at 10 metres depth and possibly missing the surface-living swarms of the copepod (Rae and Rees, 1947). It is not possible to discuss here in detail the effect this movement may have had on the distribution of other organisms, but Lucas (1941 and 1942) drew attention to the comparative scarcity of several southern phytoplankton species in 1939, and their relative increase in the north and north-east.

On the other hand, Lucas (1941 and 1942) found the central area of the North Sea to be characterized by a poor population of diatoms and dinoflagellates after the original outburst, and Fraser (1937) noted that the plankton associated with *S. setosa* is " never of a very rich nature." These observations are particularly interesting in view of the work of Russell (1936*b*) and Cooper (1938) in the English Channel, where phosphate-poor water is typified by the dominance of *S. setosa*, while both Kemp (1938) and Russell (1939) demonstrated the coincidence between poor brood years of young fish and low phosphate content. Graham's work (1938) on the origin of nutrient salts in the Southern North Sea shows the biological importance of the supply of phosphate which comes from the north into the S.W. Dogger Bank swirl, and it seems likely that the varying numbers of north-western forms found " invading " the waters more typically populated by *S. setosa* and its associates should provide some measure of the increments of phosphate from the north.

Apherusa clevei G. O. Sars.

This species was very rarely recorded north of the Forth–Skagerrak line. While it was occasionally associated with a dominant *Sagitta elegans* population off the Forth, during the autumn and winter by far the greater bulk of the stocks occurred in "*setosa*" water ; like *S. setosa* it was less abundant off the continental coasts. Tesch (1910) described it as breeding in the North Sea during the greater part of the year and, finding it absent from the Belgian area, came to the conclusion that it did not enter the North Sea from the English Channel. We did find it in the southernmost parts of the North Sea but never in any quantity, and it would appear that recruitment of the populations via the Channel inflow is not of major importance. We have noted earlier that its denser patches were found off the Humber, over the north-eastern part of the Dogger Bank and off the Forth, which may indicate the importance of swirls in the distribution.

The North-eastern Region.

By far the greater part of the North Sea populations of the two euphausians *Meganyctiphanes norvegica* M. Sars and *Thysanöessa raschii* M. Sars were found within a broad zone off the Norwegian coast, including the Skagerrak; they had, during this survey, a very similar distribution. In the Skagerrak area dense swarms of both were often taken, whereas further north, off Bergen, Meganyctiphanes was more abundant; in August in both years pure populations of Meganyctiphanes were recorded there. Meganyctiphanes was already known to spawn in Norwegian waters (Hjort and Ruud, 1929), and we have also shown that *T. raschii* almost certainly does so, particularly in the mouth of the Skagerrak (in 1939). Their larvae, therefore, will be dispersed by the same current systems. Einarsson (1945) has suggested that the extensive cyclonic circulation in the Norwegian Sea east of Iceland probably contains the larvae of Meganyctiphanes produced off the southern slopes of this sea, and that in this swirl the bulk of the stock is finally returned to the place of origin. Before this can be checked, however, we require much more extensive data from the Norwegian Sea.

The two copepods *Euchaeta norvegica* and *Calanus hyperboreus* are also characteristic of and reproduce within these north-eastern waters, and Rae and Rees (1947) have shown that Euchaeta is particularly often associated with Meganyctiphanes. These two copepods were not found, however, at our sampling level in the north-west, where the two euphausians were quite common but never abundant.

The Southern Region.

Phthisica acaudata (*Gronovius*).

The main concentrations were contained in an area comprising the Southern Bight and Heligoland Bight and a zone off the North Jutland coast extending into the Skagerrak, so that it was typical of the waters to the south and east of the central North Sea water; it was, of course, often accompanied by small numbers of Sagitta. It cannot, however, be considered as mainly restricted to Flemish water, since, particularly during the summer months, it was quite widespread between the Dutch and East Anglian coasts. Tesch (1910) in fact described it as living in the "shallower waters off the eastern and southern shores of the North Sea." Rae and Rees (1947) mentioned some of the similarities and dissimilarities between the distribution of Phthisica and *Corycaeus anglicus*, which they found particularly abundant in the coastal waters, and they concluded that the copepod was more particularly to be associated with the diatom *Biddulphia sinensis*. The caprellid, by contrast, was situated more offshore. We have already noted how, during 1938, Phthisica appeared in the plankton of these coastal waters in a south to north succession as the season advanced, and an interesting parallel between Biddulphia (Lucas, 1941) and Phthisica was that both organisms were found off the Heligoland Bight in September, 1938 (Phthisica also being recorded further south), followed in October by their appearance together off the North Jutland coast. Earlier in the season (in May and June) they had occupied a more southerly area between the Dutch and East Anglian coasts. Of these three forms, Phthisica is most readily to be associated with the position and flow of the waters arriving in the Southern Bight from the English Channel, although it is by no means so certain that Phthisica arrives from there. It is a tychopelagic organism, and may be brought to the surface by the turbulence due to a strong flow into the area. It might thus prove useful as an indicator of vertical water movement within these relatively shallow areas, and might provide useful corroborative evidence for the renewal of nutrient salts in the surface layers on which local diatom flowering may often depend. Lucas (1941) has earlier commented on the similar value of the diatom *Paralia sulcata*, which may be swept into the upper water layers " at times of extensive disturbance." It may, however, also be (see below) that the movements of Phthisica can be used as indications of the nature and direction of the Channel flow itself. Thus, there is some evidence that its numbers, and particularly its changes in distribution, are related to the varying Channel flow over the period 1932–39 (*cf.* Henderson and Marshall, 1946, Plates cxli and cxlii, and Lucas and Rae, text-fig. 12).

General Remarks.

It would seem that we have to deal with the interplay of at least four different water masses which are constantly in motion, merging sometimes abruptly and at other times more gradually. At the level of 10 metres we see a rather surprisingly small central mass of " North Sea " water proper flanked in the north-west by more saline water containing a generally different community. Not all forms, by any means, are different. *Centropages typicus* (Rae and Rees, 1947), *Nyctiphanes couchii* and *Themisto abyssorum* among others have centres in both water masses. There are of course, many forms, such as Pseudocalanus and the Cladocera, which do not readily relate to either area, although there may be distinctive stocks (discoverable by more detailed research), such as those shown by Wimpenny (1946) and Lucas (1941, 1948) for *Rhizosolenia styliformis*. The central mass is again flanked in the north-east and south by other water types, and again there are species common to both ; perhaps this is less true of the north-eastern waters than the southern, although there are movements of either of these which may result in appreciable mixtures of their communities. Again further research may bring to light different features within an apparently single stock, as Lucas (1948) shows for *Biddulphia sinensis*.

Three of these four water masses closely correspond with those described by Rae and Rees (1947), the north-western, north-eastern and central masses. The southern region, in which Phthisica was found to originate, does not quite correspond with their south-eastern one indicated by Corycaeus, which undoubtedly appears, where it is abundant, to denote coastal water, whilst Phthisica most likely indicates those waters most influenced by the Channel stream.

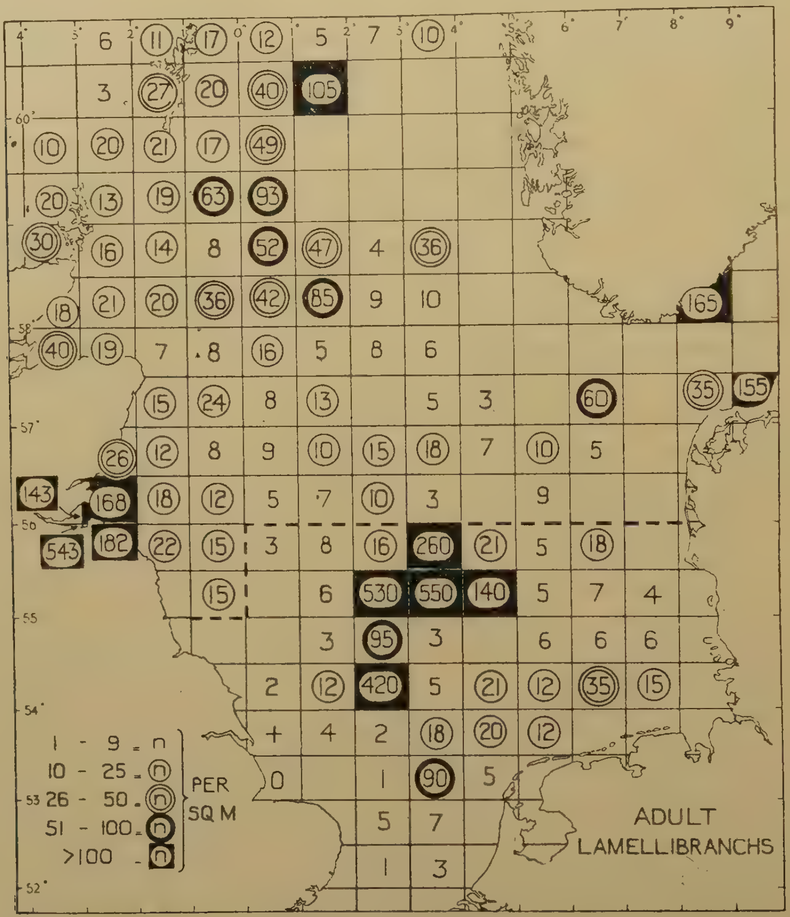
Such details will be discussed more fully in a later paper by Rae and Lucas discussing the plankton as a whole in relation to its environment. Meanwhile, it is obvious that three of these four water masses are closely related to the entrances and exits from the North Sea, the central water in some ways being seen as a reservoir containing indigenous forms such as *S. setosa*, but also partly populated as the result of inflow from the neighbouring water masses. When seen in this way it seems reasonable to suggest that in these changing interrelationships there should be one of the keys to the understanding of water movements without as well as within the North Sea. Meanwhile, despite the importance of such changes, one of the more remarkable features of the survey has been, as was also shown by the work of Rae and Rees (1947), the similarity in the broad features of the two years. A good example is provided by the data for August in 1938 and 1939 (Text-figs. 4 and 5). Such similarities do suggest that the plankton records provide evidence of an underlying theme upon which detailed variations are played.

We may now consider one or two special aspects of the zooplankton in relation to the phytoplankton. In one sense it can be said that phytoplankton populations make better indicators than the animals in that they seem to be more sensitive to changes in the environment. Yet little is known of the causes leading to the often very rapid succession in phytoplankton populations, and Gran (1912) concluded that large animals would prove to be more practical indicators than the plants. He did, however, draw attention to the importance of the species of Ceratium in providing an indication of the boundaries between water types. There is considerable evidence from this survery of a correlation between the Sagitta boundaries and the distribution of some of the dinoflagellates, to which Lucas (1942) has earlier referred. He showed that there were two main areas of dinoflagellate production, one in the north-western North Sea and the other in the south-eastern. In September, 1938, when the boundary between the populations of *S. elegans* and *S. setosa* became clearly defined, the transition between these species exactly marked the edge of the abundant *north-western* stock of *Ceratium fusus*, this edge being indicated by a sudden and marked drop in the numbers of the dinoflagellate. A similar and hardly less striking correlation can be seen for *Ceratium tripos* and *C. furca*. Earlier in July and August the eastern edge of the *elegans* population on the Pentland-Bergen line also coincided with that of *C. fusus*. Further south in Scottish waters, although *S. elegans* was not yet sufficiently well represented on our lines for the boundary between it and *S. setosa* to be shown, the western edge of the "*setosa*" population (particularly in August) was remarkably close to the edge of the north-western complex of *C. fusus*. In the earlier section discussing *S. setosa* as an indicator special note was made of its abundance in the more *central* areas where the dinoflagellate production was usually poor. It is further significant that it is just in the rich *south-eastern* area of dinoflagellates, the Flemish and German coastal area, that *S. setosa* is least abundant, perhaps indicating a broad inverse correlation between Sagitta and the dinoflagellates. On the other hand, there are times (*e.g.* October and November, 1938) when the Ceratia are scarcer on the *elegans* side of the north-western boundary. These were times of mixing of the two Sagitta populations, probably denoting water mixing which might have provided phosphates at the surface for a secondary phytoplankton growth. Lucas (1941) found the diatom Paralia to extend rapidly at the surface in these months. Similarly, the records for July and August in 1939 show a rather less definite correlation than in 1938, and it was during these months that a mass extension of *S. setosa* into the eastern part of the "*elegans*" complex took place.

Whilst some of the correlations between the dinoflagellates and Sagitta distributions may only arise under relatively stable hydrological conditions, the results suggest that such sharp boundaries must be related to equally sharp environmental changes. In the other parts of the North Atlantic where *S. elegans* breeds successfully, the work of Huntsman (1919), Bigelow (1926), Russell (1936) and Redfield and Beale (1940) indicates that it is particularly prolific in regions characterized by swirls or "dead water" which concentrate the reproducing members of the population. Clarke, Pierce and Bumpus (1943), in their investigations on *S. elegans* over Georges Bank, came to the conclusion that it was abundant in this area, "first, because the relative permanence of this water mass allows it to accumulate there; second, because water of harmfully high temperature and salinity from the south is excluded; and third, because some indirect influence from the shore or bottom absent in the deeper water to the north favours its reproduction and growth." In our region it is likely that the Moray Firth and Firth of Forth swirls play an important part in concentrating the breeding population of *S. elegans* and other organisms, but these physical and hydrological features alone can hardly account for the sharp division between the "*elegans*" and "*setosa*" water types. Fraser (1939) expressed this by concluding that "the very distinct separation of forms from one water mass to another does mean some biological change that at present cannot be defined in chemical and physical terms and yet nevertheless is a very real change of vital importance." The evidence given above is further suggestive of the existence of those biological factors which Lucas (1938, 1947) has considered in a special study. If, in the future, it should be possible to obtain, in the same place and at the same time, detailed hydrological data for comparison with our plankton records, it might be possible to make for the first time some of the necessary comparisons.

PLANKTONIC LARVAE AND THE BOTTOM FAUNA.

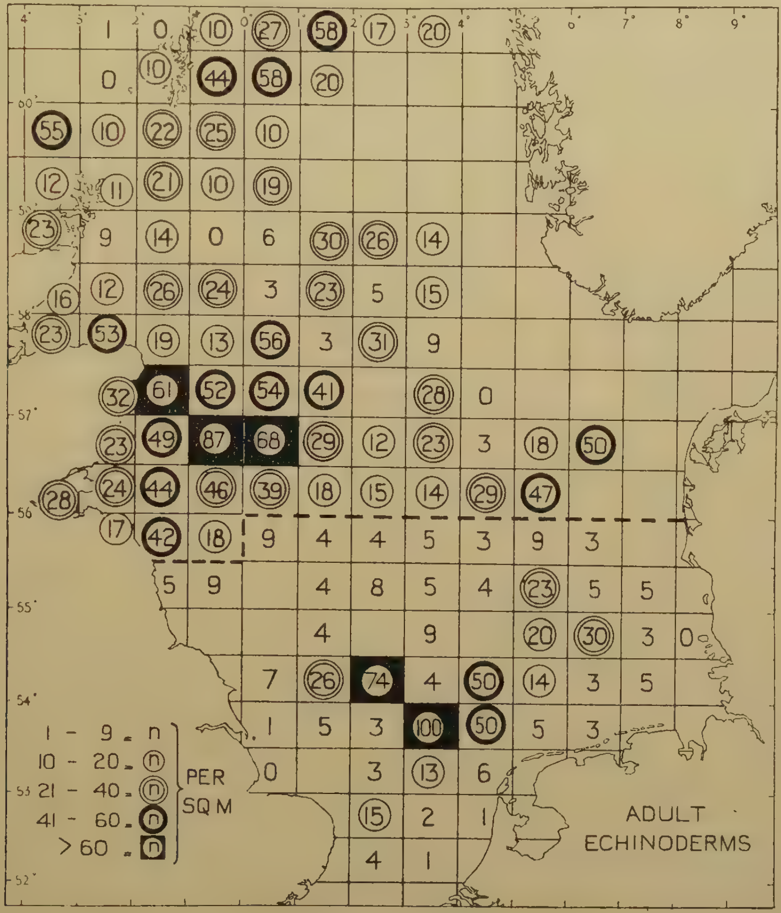
The great difference which exists between the number of planktonic larvae produced by a benthic organism and the number which eventually settle on the bottom is brought about by many environmental factors. Thorson (1946) has shown clearly the complex nature of any attempt to obtain a measure of this difference. The present results, providing the first overall monthly picture of some North Sea larval populations at 10 metres, may be tentatively considered in relation to (1) the general distribution of the bottom fauna, (2) the effect of environmental conditions such as temperature on breeding, and (3) the influence of currents on the distribution of the larvae.


ADULT LAMELLIBRANCHS
1 - 9 = n
10 - 25 = ⓝ
26 - 50 = ⓝ
51 - 100 = ⓝ
>100 = ⓝ
PER SQ M
60°
57°
56
55
54°
53
52°
6 11 17 12 5 7 10
3 27 20 40 105
10 20 21 17 49
20 13 19 63 93
30 16 14 8 52 47 4 36
18 21 20 36 42 85 9 10 165
40 19 7 8 16 5 8 6
15 24 8 13 5 3 60 35 155
26 12 8 9 10 15 18 7 10 5
143 168 18 12 5 7 10 3 9
543 182 22 15 3 8 16 260 21 5 18
15 6 530 550 140 5 7 4
3 95 3 6 6 6
2 12 420 5 21 12 35 15
+ 4 2 18 20 12
0 1 90 5
5 7
1 3

TEXT-FIG. 6.—Chart showing the numbers of adult lamellibranchs per square metre for each international square in the North Sea, as determined by Davis (1923, 1925) for the south, and Stephen (1933, 1934) to the north of the broken line.

The quantitative surveys of the bottom fauna by Davis (1923, 1925) and

Stephen (1933, 1934) contribute some data towards the first. Their data for adult lamellibranchs and echinoderms have been plotted as numbers per square metre in Text-figs. 6 and 7. It will be obvious from the time factor alone that only very general comparisons should be drawn between these results and our larval data, and even if the times of the three investigations tallied more closely, we should still be hesitant in relating the densities of adults to the numbers of larvae. We have relatively little knowledge of the egg productions of the various species which make up the bottom fauna and no data as yet on the specific constitution of the larval populations,[1] but the comparison may be useful as a preliminary attempt.


4° 3° 2° 1° 0° 1° 2° 3° 4° 5° 6° 7° 8° 9°
60°
59°
58°
57°
56°
55°
54°
53°
52°
1 0 10 27 58 17 20
0 10 44 58 20
55 10 22 25 10
12 11 21 10 19
23 9 14 0 6 30 26 14
16 12 26 24 3 23 5 15
23 53 19 13 56 3 31 9
32 61 52 54 41 28 0
23 49 87 68 29 12 23 3 18 50
28 24 44 46 39 18 15 14 29 47
17 42 18 9 4 4 5 3 9 3
5 9 4 8 5 4 23 5 5
4 9 20 30 3 0
7 26 74 4 50 14 3 5
1 5 3 100 50 5 3
0 3 13 6
15 2 1
4 1
1 - 9 . n
10 - 20 . ⓝ
21 - 40 . ⓝ
41 - 60 . ⓝ
> 60 . ▣
PER SQ M
ADULT ECHINODERMS

Text-fig. 7.—Chart showing the numbers of adult echinoderms per square metre for each international square in the North Sea, as determined by Davis (1923, 1925) for the south, and Stephen (1933, 1934) to the north of the broken line.

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[1] Mr. C. B. Rees at the Leith Laboratory is at present investigating the possibility of identifying the larval lamellibranchs, etc., in the recorder material.

For the adult lamellibranchs (Text-fig. 6) the richest areas in order of densities are the Dogger Bank, the northern North Sea, the waters off the Forth, and an area off the Dutch coast extending into the Heligoland Bight. It will be recalled that the main centres of larval concentration were over the three former areas and over and around the Great Fisher Bank. The presence of extensive and dense patches in this bank region in June and July of both years at first sight does not agree with Stephen's data. The lamellibranch fauna of the Great Fisher Bank actually forms part of the faunistic area which Stephen has called the Offshore Zone, and he characterized it as having no dominant species and a low density. There may well have been a change in the adult populations of this area since the time of the Scottish survey, but it also seems possible that some of the larval concentrations over the Fisher Bank may be produced by the dense population of adults recorded by Davis (1923) on the north-eastern half of the Dogger Bank. The local current systems might well produce the requisite drift ; if so a fair proportion of young stages of *Spisula spp.* would be expected.

The denser populations of adult echinoderms (Text-fig. 7) are found in the north-western North Sea and in an area lying off the south-eastern side of the Dogger Bank, which extends eastward into the Heligoland Bight and southwards into the Southern Bight. This shows a close correspondence with the main centres of distribution of the larvae, although it should be noted that the south-eastern larval concentrations were many times more numerous than those of the north-western North Sea and would appear to indicate a denser adult population. Reference to Text-figs. 2 and 3 in this paper and also in ' Bulletin ' No. 6, showing the average monthly catches on the Bremen and Rotterdam routes from Hull, reveals that there has been a succession of good brood years in the south-eastern area from 1936 onwards. Unfortunately we have no corresponding data for the north-western North Sea, but it may be that part of the great difference between the two areas in recent years was due to more successful reproduction in south-eastern waters. It may also be significant that, where the two surveys overlap (between latitudes 56° 30′ and 55° 30′ N.), Stephen's figures are consistently higher than those of Davis, being five times larger on an average, so that the south-eastern adult populations of 1924 may have been unusually low. There can be no doubt that bottom faunas are subject to great change from year to year, and it is further illuminating that Thorson (1946) finds these annual fluctuations to be greater for organisms having a long planktotrophic phase. The majority of echinoderms fall into this category.

The great concentrations of decapod larvae in the Southern North Sea, in contrast to the smaller concentrations in Scottish waters, parallels what has been described for the echinoderms. Unfortunately grab surveys cannot give a reliable estimate of the more active " Natantia," but the results certainly show that the Southern and Heligoland Bights in particular must support a rich bottom fauna of decapods, and re-emphasize their importance as good feeding grounds for fish.

When describing the distribution of the echinoderm and decapod larvae in the Southern North Sea a south to north succession of the main concentrations was noted, the former larvae providing a very clear-cut instance (p. 188). A great part of these larval swarms were produced within the area of the northgoing drift of water which forms the Jutland current, and it is most likely that larvae produced on the more southerly grounds spread northwards with this current; yet it is also possible that there might be a south to north succession in the reproduction of the adults. The yearly cycle of bottom temperatures as shown in the 'Bulletin Supplementaire' published by the International Council (1908) lends some support to the latter suggestion. In general there is a steady decrease in bottom temperatures from the southernmost North Sea north-eastwards into the Skagerrak. Orton (1920) has discussed the relations between temperature and the breeding season, and Thorson (1946) has made detailed investigations in the Kattegat, differentiating between the temperatures which ripen the gonads and those which stimulate the actual liberation of their products. It is interesting to compare Thorson's results for the Kattegat during 1938 with our data from the Skagerrak, where the peak period for echinoderm larvae occurred in August. In the Kattegat the greater numbers of echinoderm species are autumn spawners, and spawning sets in after the warming up of the "Kattegat water layers." It is evident that this stimulating increase in temperature takes place later in the year than did that in the Skagerrak.

Planktonic larvae of benthic organisms may often become dispersed into areas where conditions are less favourable for development, and any local conditions of circulation which may concentrate or retain larvae in suitable areas must play an important part in the maintenance of the bottom fauna. It is therefore significant that the main concentrations of lamellibranch larvae occur in areas often characterized by well-marked swirls, *e.g.* the Dogger Bank, the north-western North Sea and the Great Fisher Bank (Böhnecke, 1922). The distribution of adult echinoderms, again, which we have seen to be most abundant in Scottish waters (particularly in the more southerly regions) and in an off-Dogger area, further suggests the importance of local eddies in these parts in retaining the larvae sufficiently long in one place for the completion of their planktonic life. Thorson (1946) quotes figures for the duration of the pelagic life of echinoderm larvae, and has shown that the majority have a relatively long planktotrophic existence, the extent of which depends on temperature, available food and the presence or absence of a suitable substratum on which to settle; in these latitudes it would appear to be anything from a few weeks to two months. The well-marked and persistent swirl in the Heligoland Bight, as well as those of the Dogger, which may vary considerably, are no doubt factors in the maintenance of the south-eastern echinoderm populations; without such swirls it is not clear how the adult populations could be maintained in the face of a current flowing regularly over them. Kramp (1927) came to the conclusion that owing to the Heligoland Bight swirl, "Horn Reef and the west coast of Jutland receive practically no supply of medusae from the Bay of Heligoland, for if so, several of the species indigenous there would have been found." As with hydromedusae, so also with the larvae caught up in this swirl: they are retained within it long enough to complete their planktonic existence.

Orton (1937) has remarked that "there can be little doubt that immense quantities of larval fish foods in the form of bivalves and worms become concentrated in these swirls or eddies. Where subsurface conditions are suitable, as over the Dogger Bank, in the Moray Firth, in the mid-east Scottish coast and other areas, the larvae settle out of the plankton to form rich feeding grounds for fish." The association between submarine banks and water swirls is familiar, and it is therefore not surprising that many banks support a rich benthic fauna. The flow of water into well-marked coastal profiles such as bights or firths also generates swirls, again creating conditions for heavy spat falls wherever the nature of the bottom permits. In general, the distribution of the economically more important larvae in this survey may be said to have borne out these conclusions very well.

SUMMARY.

1. The distributions of various zooplankton organisms (other than Copepoda and young fish) collected in the North Sea by the Continuous Plankton Recorder from January, 1938, to August, 1939, are illustrated (Plates LXXXIX–CVIII) and reviewed in comparison with earlier work (pp. 175 to 189).

2. Whilst some of them, particularly groups not identified to species, *e.g.* the Cladocera, had a generalized distribution, the others could be grouped in relation to different water masses, and their monthly variations in distribution reviewed and contrasted.

3. These water masses comprised: (1) a north-western, with *Sagitta elegans*, *Thysanöessa inermis* and *Clione limacina* among its most typical indicators; (2) a north-eastern, with *Meganyctiphanes norvegica* and *Thysanöessa raschii;* (3) a central, with *Sagitta setosa* and *Apherusa clevei;* and (4) a southern with *Phthisica acaudata* (pp. 190 to 203).

4. With the exception of the last, these correspond closely with those of Rae and Rees (1947) for the Copepoda and with the generalized picture of Russell (1939). Phthisica may prove useful as an indication of the influence and variations of English Channel water.

5. A preliminary comparison is made of records of the planktonic larvae of lamellibranchs and echinoderms with such knowledge as is available of the adult distribution on the bottom (Davis, 1923 and 1925, and Stephen, 1933 and 1934). The occurrence, breeding, movement and deposition of such larvae is discussed in relation to their environment (pp. 206 to 210).

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EXPLANATION OF PLATES LXXXIX–CVIII.

PLATES LXXXIX–XCI.

Charts showing the distribution of Sagitta spp. (p. 175) month by month from January, 1938 to June, 1939. Numbers and symbols denote the varying numbers on each ten-mile block (for scales see insets). Where more than one record has been obtained in any month they have usually been shown "in parallel" (the earlier one above) and bracketed together. Where this has not been possible, one representative record has been shown in the usual manner and the other(s) have been shown in the margin, as in August, 1938, the numbers I and II denoting the order of the series (for dates see 'Bulletin' No. 7).

In Plate LXXXIX the species of Sagitta are not separated, but Plates XL and XLI show the distribution of *Sagitta elegans* (white numbers on black) and *S. setosa* (black on white). Part-coloured symbols denote proportionate mixtures of the two species, the numbers denoting the total combined (p. 176). The data for July and August, 1939, are shown in Plate XCVII.

Erratum.—The symbols for the first of the Pentland–Bergen records taken in October, 1938, erroneously indicate *S. setosa.* They should indicate *S. elegans.*

PLATES XCII AND XCIII.

Charts showing the distribution of the Pteropoda (p. 180), month by month from January, 1938, to June, 1939 (for scale see inset). Where two or more months have been combined the earlier records are shown above, those bracketed together occurring in the same month. See also explanation of Plates LXXXIX–XCI. The data for July and August, 1939, are shown in Plate XCVII.

PLATES XCIV–XCVI.

Charts showing the distribution of *Nyctiphanes couchii*, *Nematoscelis megalops* and *Meganyctiphanes norvegica* (p. 183) month by month from January, 1938, to June, 1939 (for scales see inset). See also explanation to Plates LXXXIX–XCI. The data for July and August, 1939, are shown on Plate XCVII. (Numbers within a double circle should be multiplied by 10.)

PLATE XCVII.

Charts continuing the data for Sagitta spp., Pteropoda, Nyctiphanes and Meganyctiphanes into July and August, 1939 (for scales see insets), but otherwise arranged as in Plates LXXXIX–XCVI.

PLATES XCVIII–C.

Charts showing the distribution of *Thysanöessa inermis* and *T. raschii* (p. 184) month by month from January, 1938 to August, 1939 (for scale see inset). Where two or more months have been combined the earlier records are shown above, those bracketed together occurring in the same month. See also explanation to Plates LXXXIX–XCI.

PLATES CI–CIII.

Charts showing the major patches of Lamellibranch Larvae (CI and p. 185), Podon spp. (CII and p. 186) and Evadne spp. (CIII and p. 186), during 1938 and 1939. Symbols are used to denote the varying quantities on each ten-mile block (see scale). Where more than one record has been used in any month, they have usually been shown " in parallel " (the earlier one above) and bracketed together. Where this has not been possible, one representative record has been shown in the usual manner and the other(s) have been shown in the margin, as in July, 1939, the symbols I and II denoting the order of the series (for dates see 'Bulletin' No. 7).

PLATES CIV AND CV.

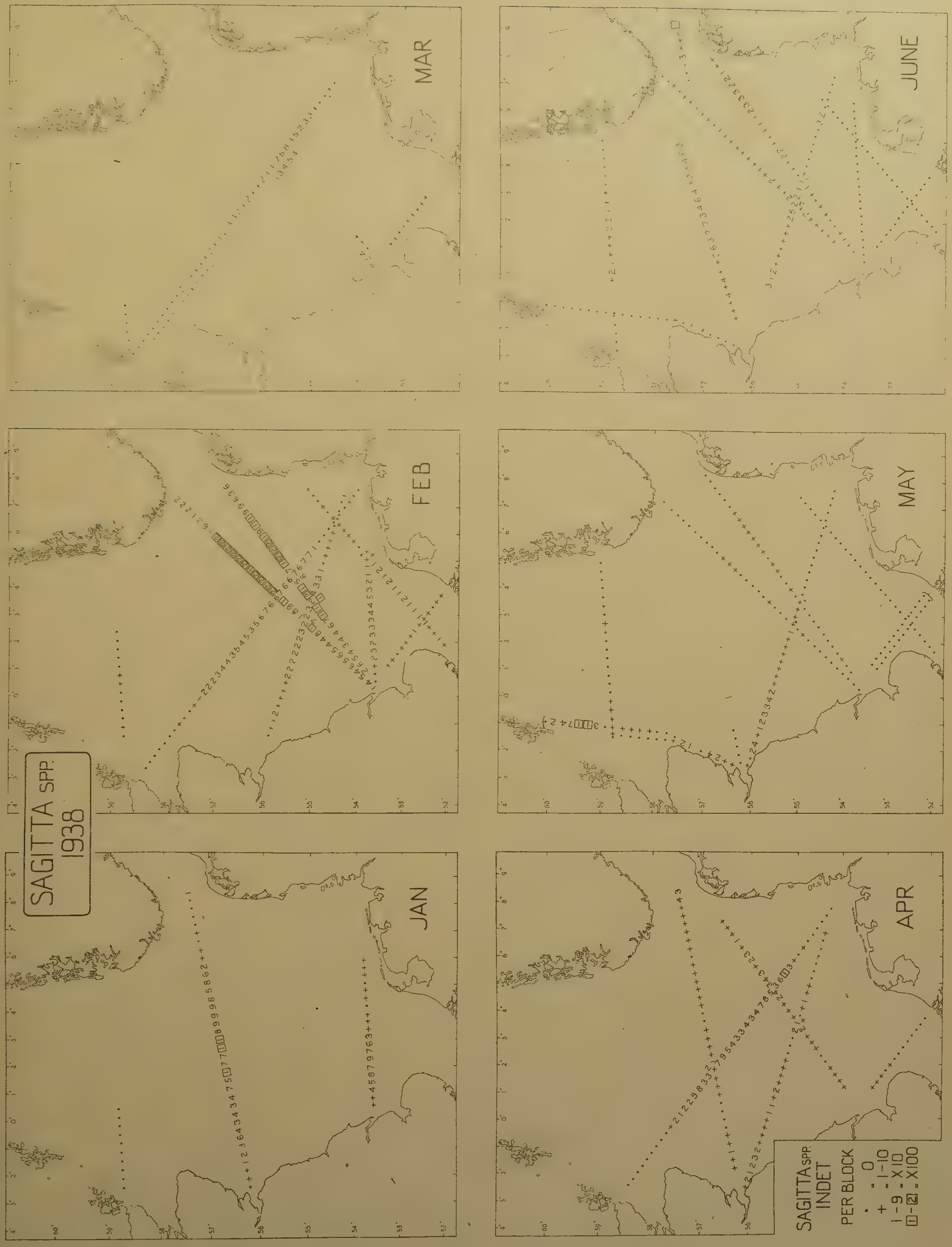
Charts showing the distribution of Amphipoda (p. 186) during 1938 and 1939 (see scale). Where two or more months have been combined, the earlier records are shown above, those bracketed together occurring in the same month. See also explanation to Plates CI–CIII.

Plate CV also shows the distribution of the major patches of Cyphonautes Larvae during the same period (see scale and general explanation, p. 187).

PLATES CVI AND CVIII.

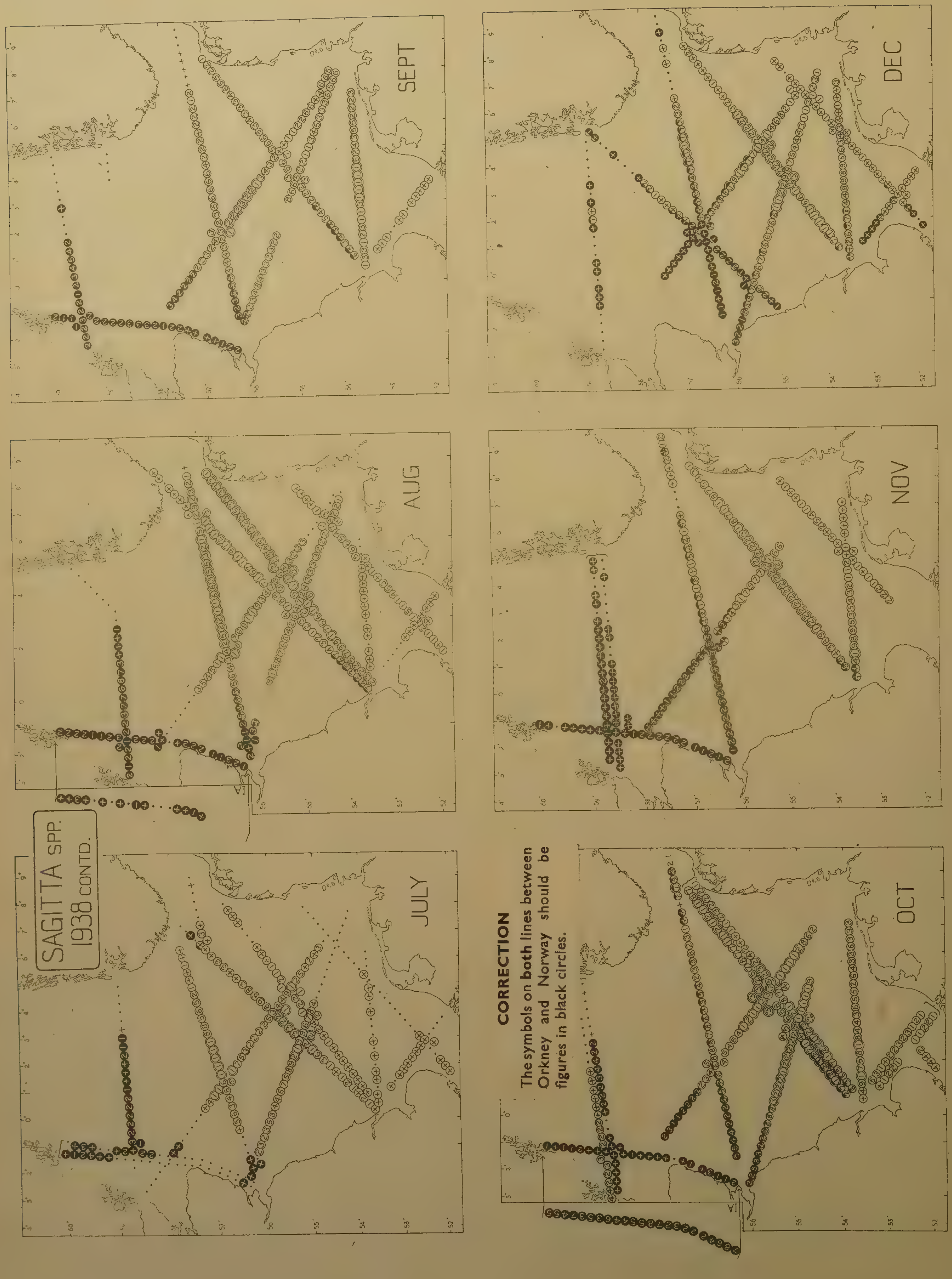
Charts showing the major patches of Decapod Larvae (CVI and p. 188), Echinoderm Larvae (CVII and p. 188) and Oikopleura spp. (CVIII and p. 189) during 1938 and 1939 (see scales and explanation of Plates CI–CIII). Where two or more months have been combined the earlier records are shown above, those bracketed together occurring in the same month.

PLATE LXXXIX



SAGITTA SPP.
1938
JAN
FEB
MAR
APR
MAY
JUNE
SAGITTA SPP.
INDET
PER BLOCK
· 0
+ 1-10
1-9 X10
1-2 X100

PLATE XC


SEPT
DEC
AUG
NOV
JULY
OCT

SAGITTA SPP.
1938 CONTD.

CORRECTION
The symbols on **both** lines between Orkney and Norway should be figures in black circles.

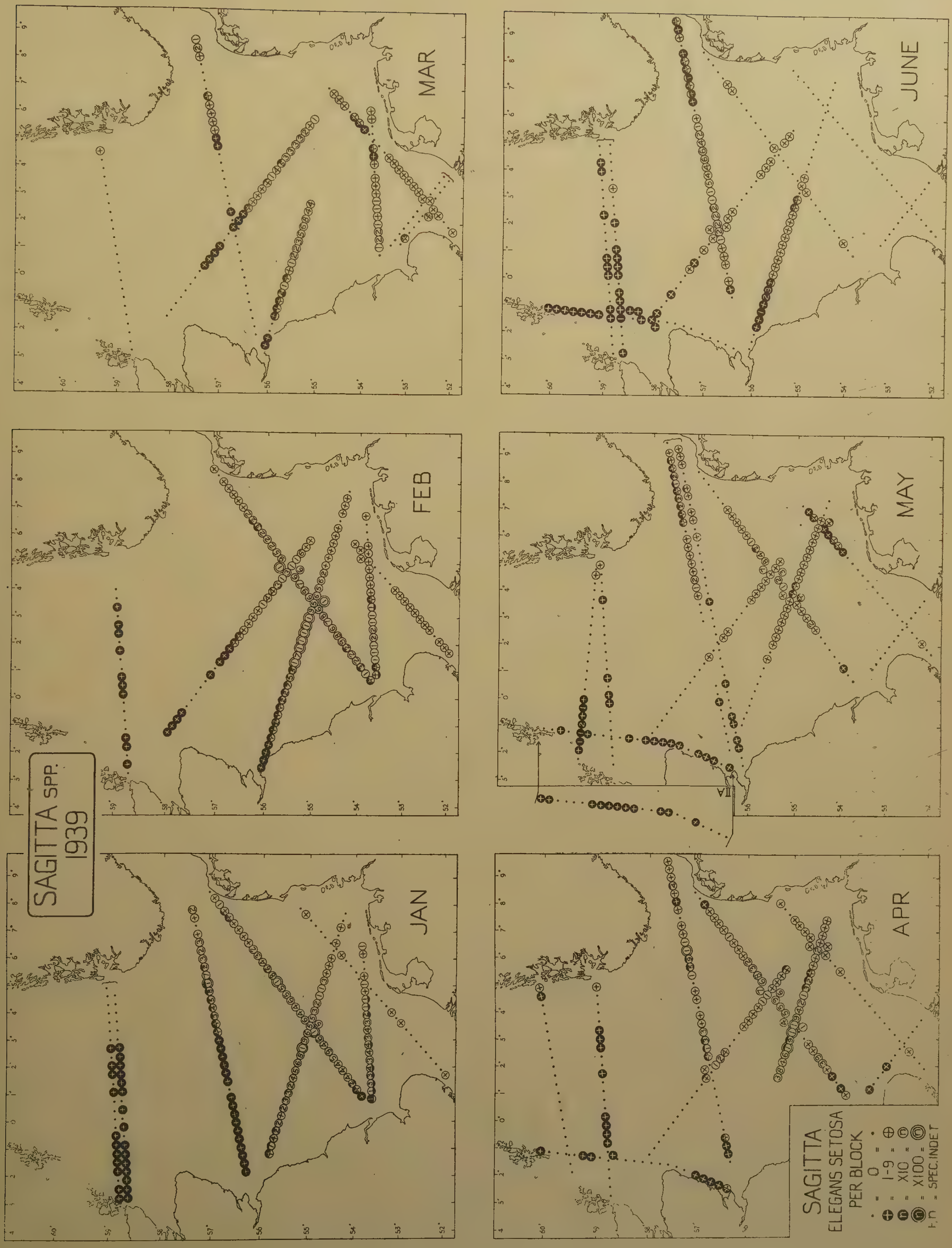

SAGITTA SPP. 1939
JAN
FEB
MAR
APR
MAY
JUNE
SAGITTA
ELEGANS SETOSA
PER BLOCK
· = 0
⊕ = 1-9 = ⊕
= X10 = ⓒ
= X100 = ◎
F.D. = SPEC. INDET.

PLATE XCII

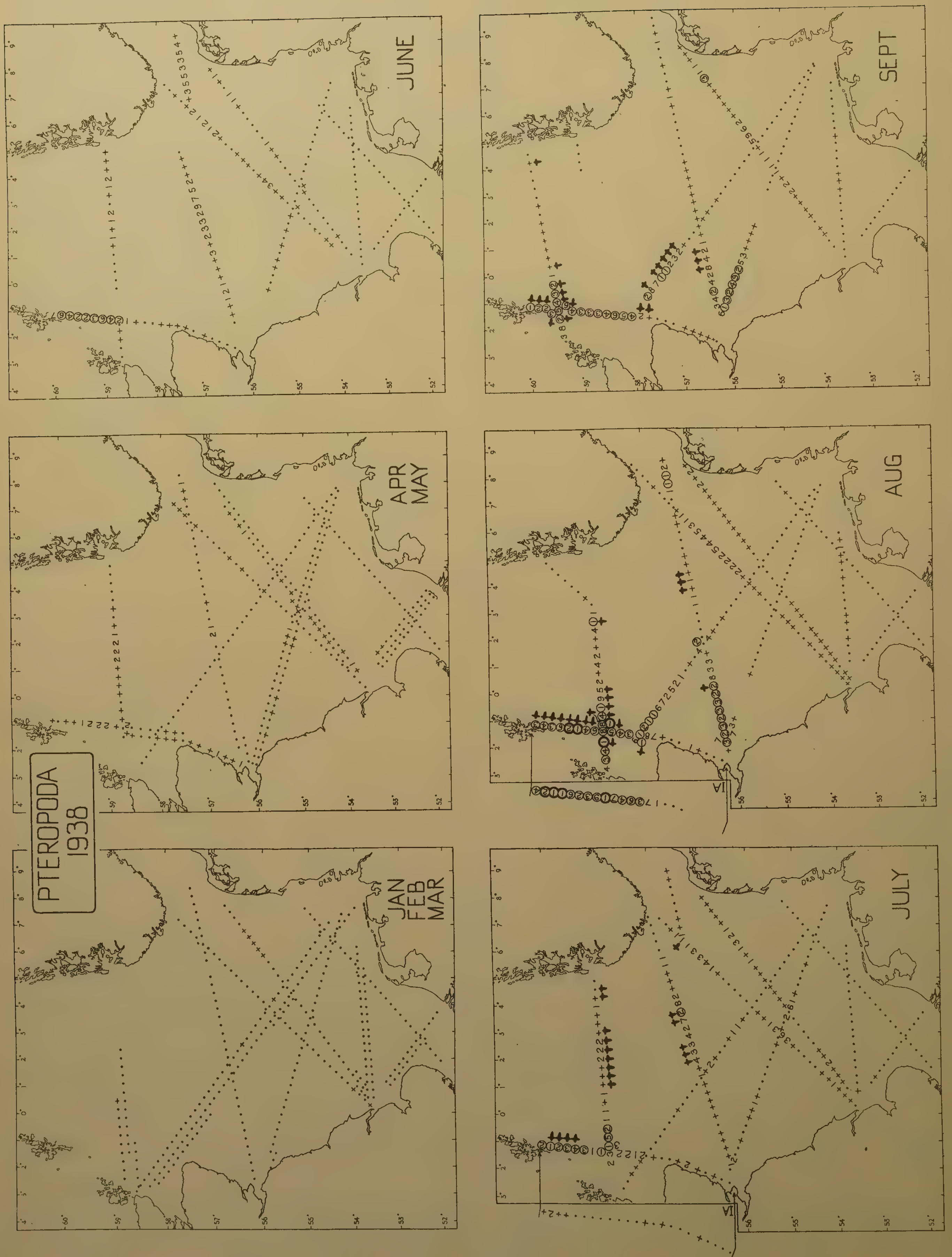

PTEROPODA 1938
JAN FEB MAR
APR MAY
JUNE
JULY
AUG
SEPT
1A
60°
59°
58°
57°
56°
55°
54°
53°
52°

PLATE XCIII

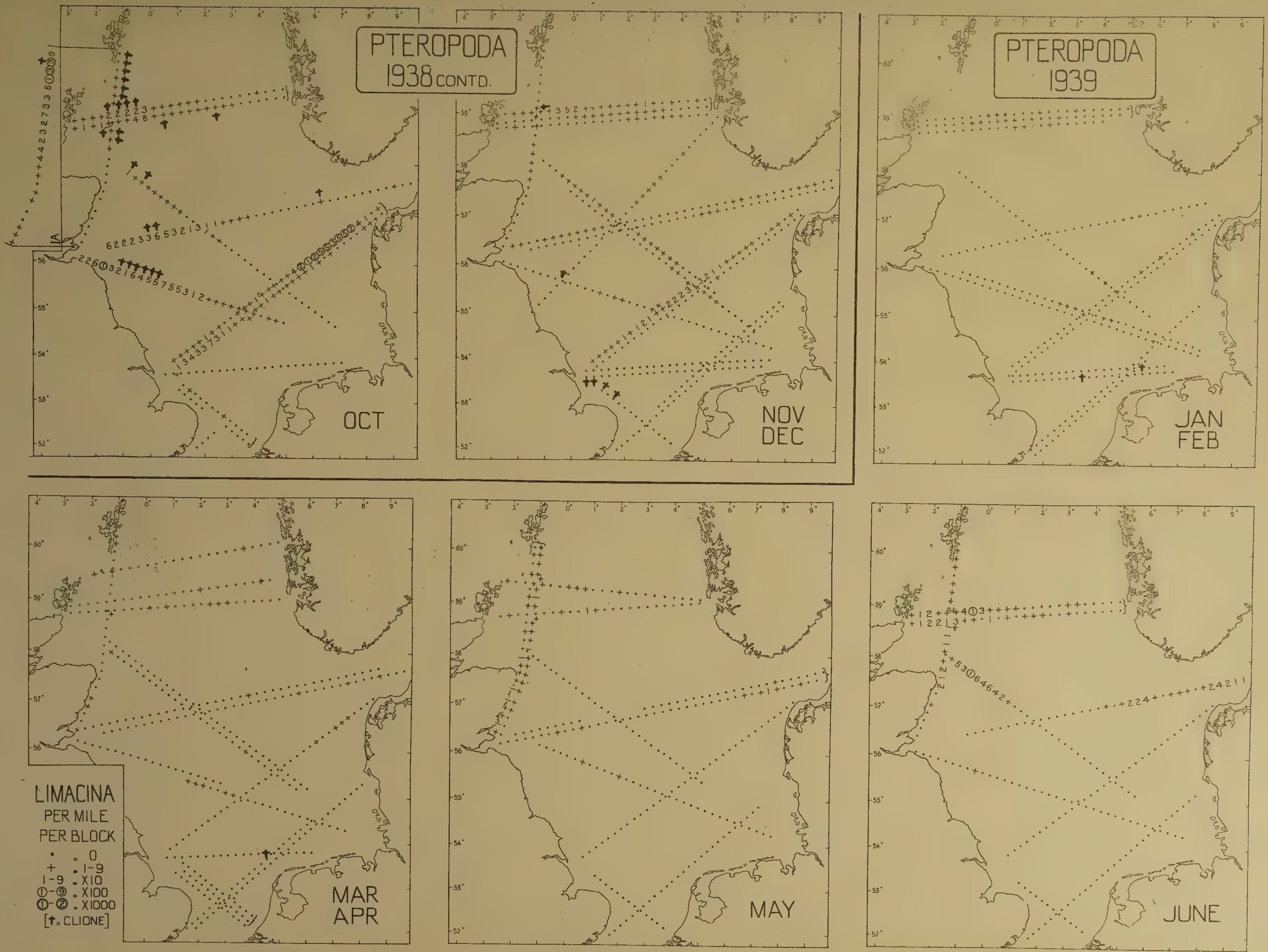
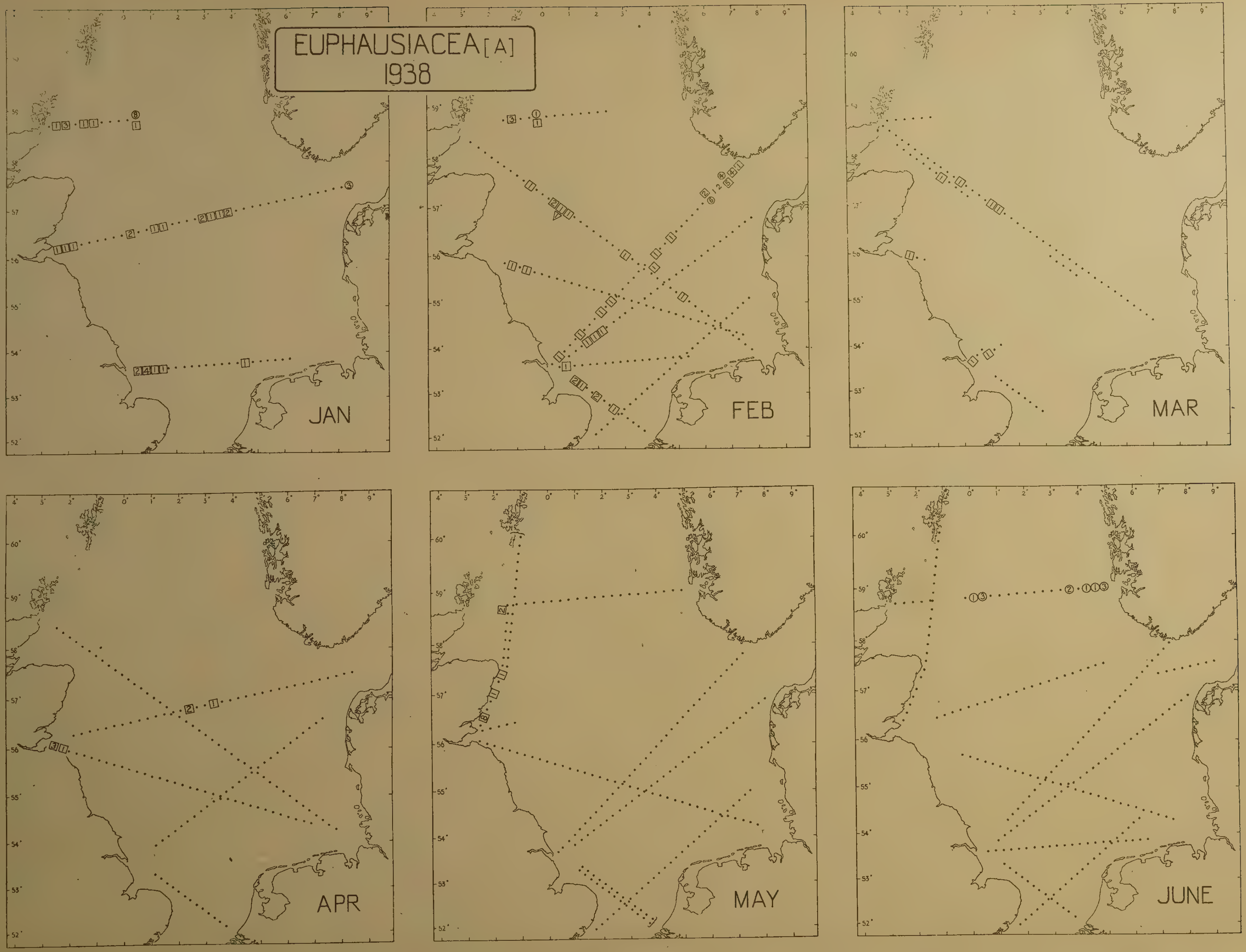

PTEROPODA 1938 CONTD.
OCT
NOV DEC
PTEROPODA 1939
JAN FEB
MAR APR
MAY
JUNE
LIMACINA
PER MILE
PER BLOCK
• = 0
+ = 1-9
1-9 = X10
①-⑨ = X100
①-② = X1000
[✝ = CLIONE]

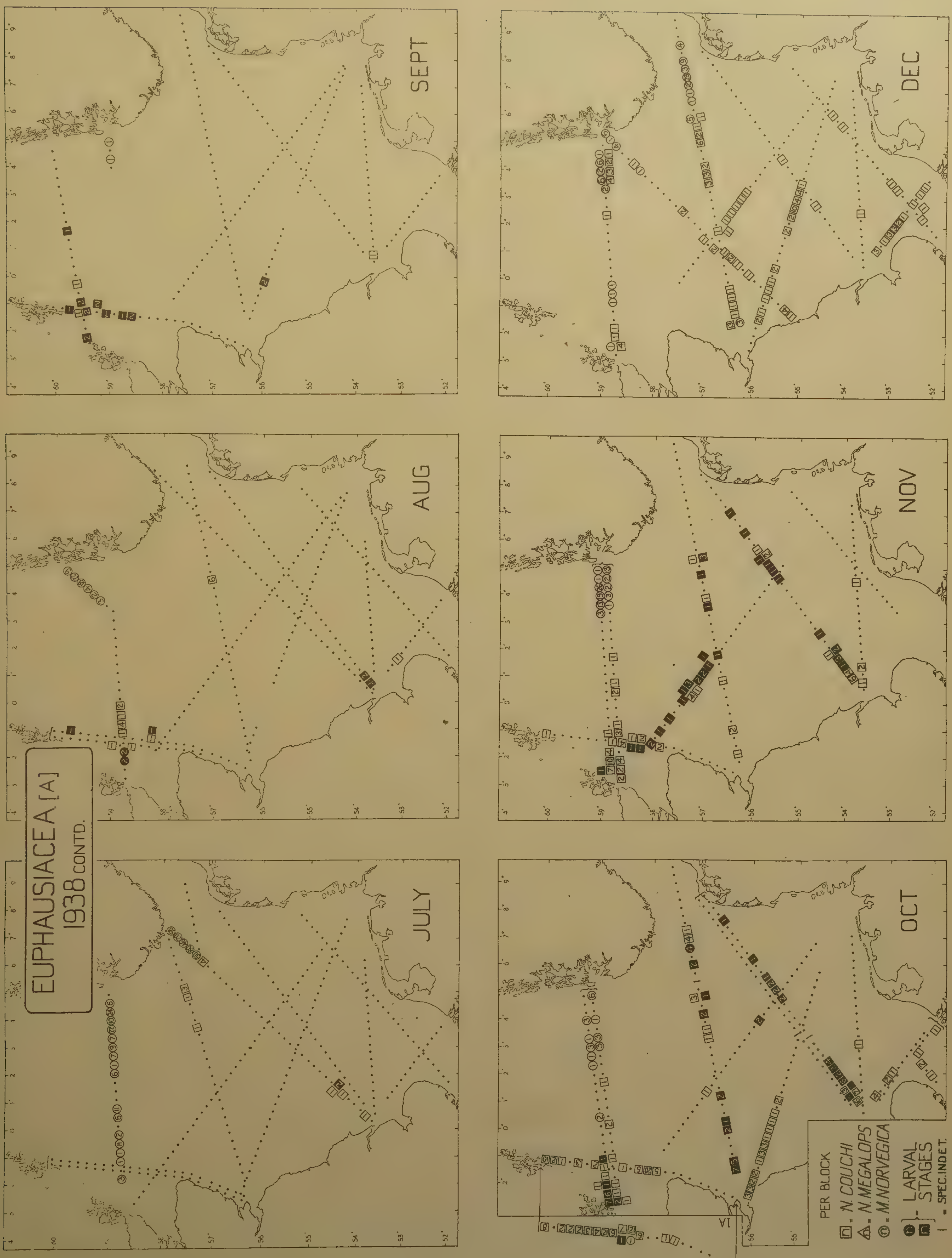
PLATE XCIV



EUPHAUSIACEA [A]
1938

JAN
FEB
MAR
APR
MAY
JUNE

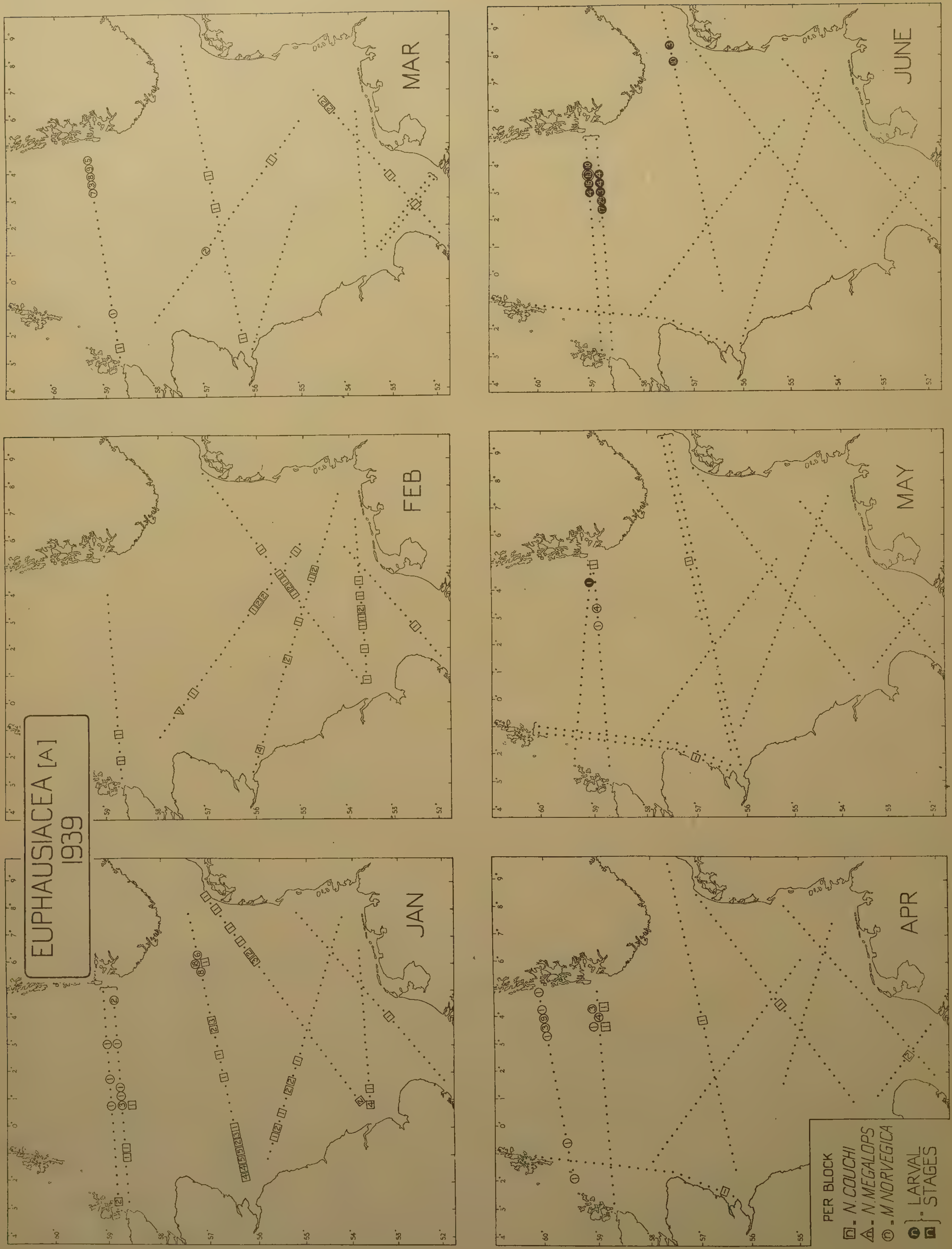
PLATE XCV

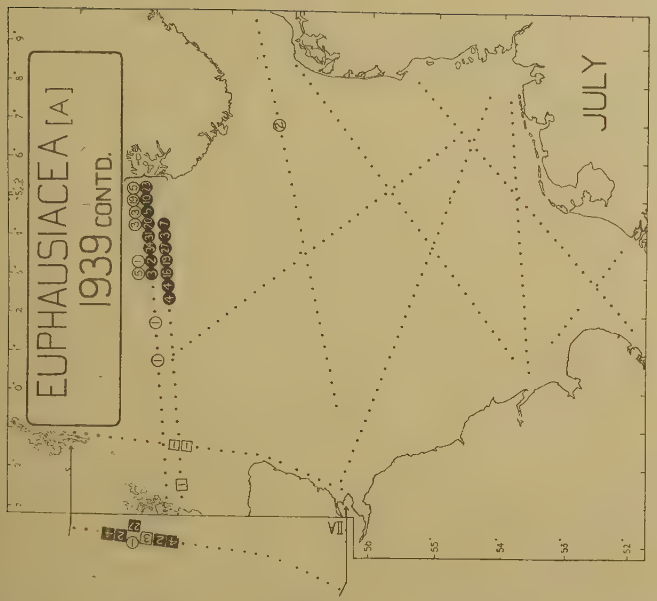


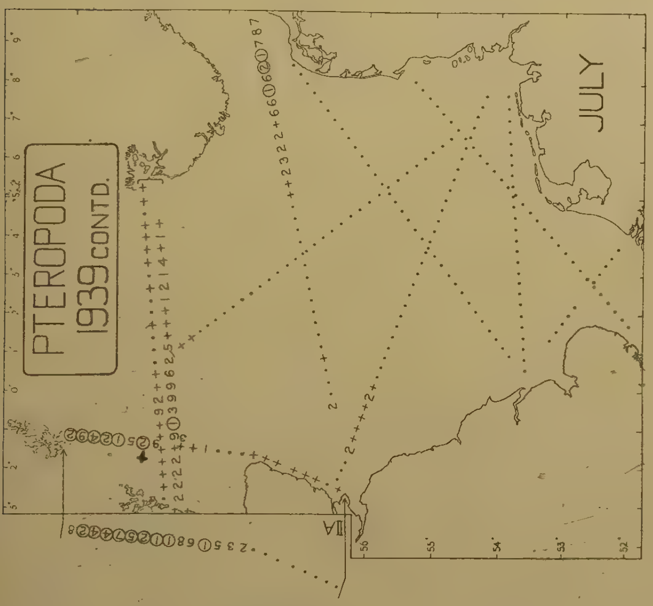
EUPHAUSIACEA [A] 1938 CONTD.

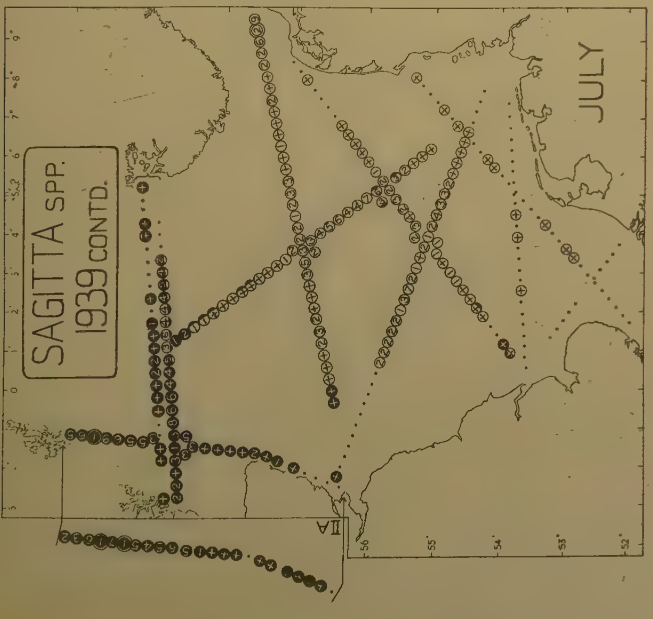
JULY
AUG
SEPT
OCT
NOV
DEC
PER BLOCK
□ - N. COUCHI
△ - N. MEGALOPS
○ - M. NORVEGICA
● ■ } - LARVAL STAGES
I = SPEC. INDET.

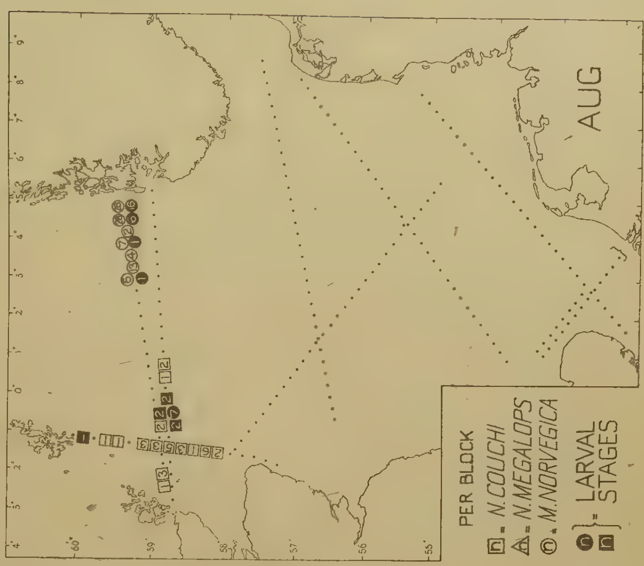
PLATE XCVI

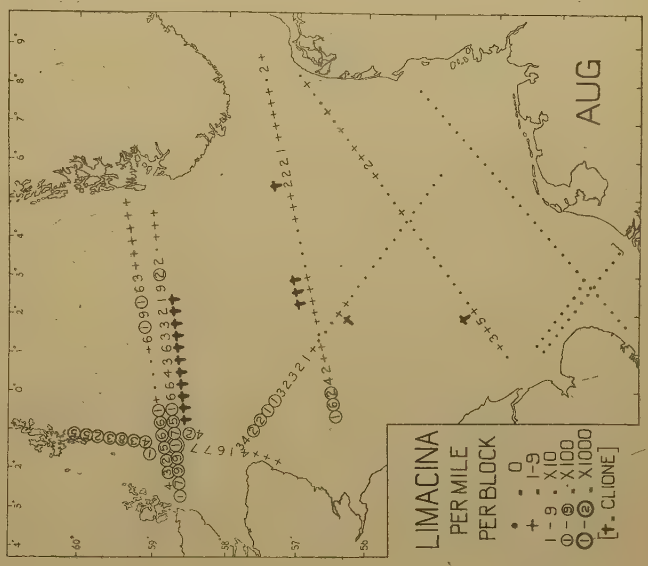

EUPHAUSIACEA [A]
1939
JAN
FEB
MAR
APR
MAY
JUNE
PER BLOCK
□. N. COUCHI
△. N. MEGALOPS
○. M. NORVEGICA
● ■ } LARVAL STAGES


EUPHAUSIACEA [A]
1939 CONTD.
JULY
VII


PTEROPODA
1939 CONTD.
JULY
VII


SAGITTA SPP.
1939 CONTD.
JULY
VII


AUG
PER BLOCK
□ . N. COUCHI
△ . N. MEGALOPS
○ . M. NORVEGICA
● ■ } - LARVAL STAGES


AUG
LIMACINA
PER MILE
PER BLOCK
• : 0
+ : 1-9
1 - 9 : X10
①-⑨ : X100
①-② : X1000
[✚ . CLIONE]

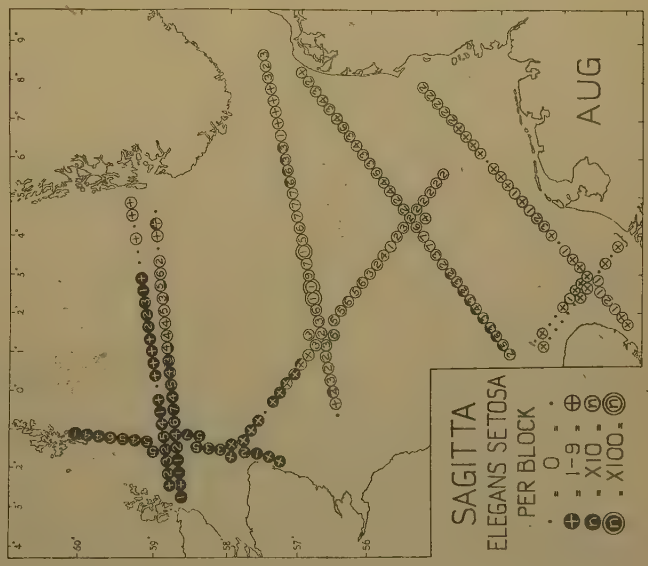
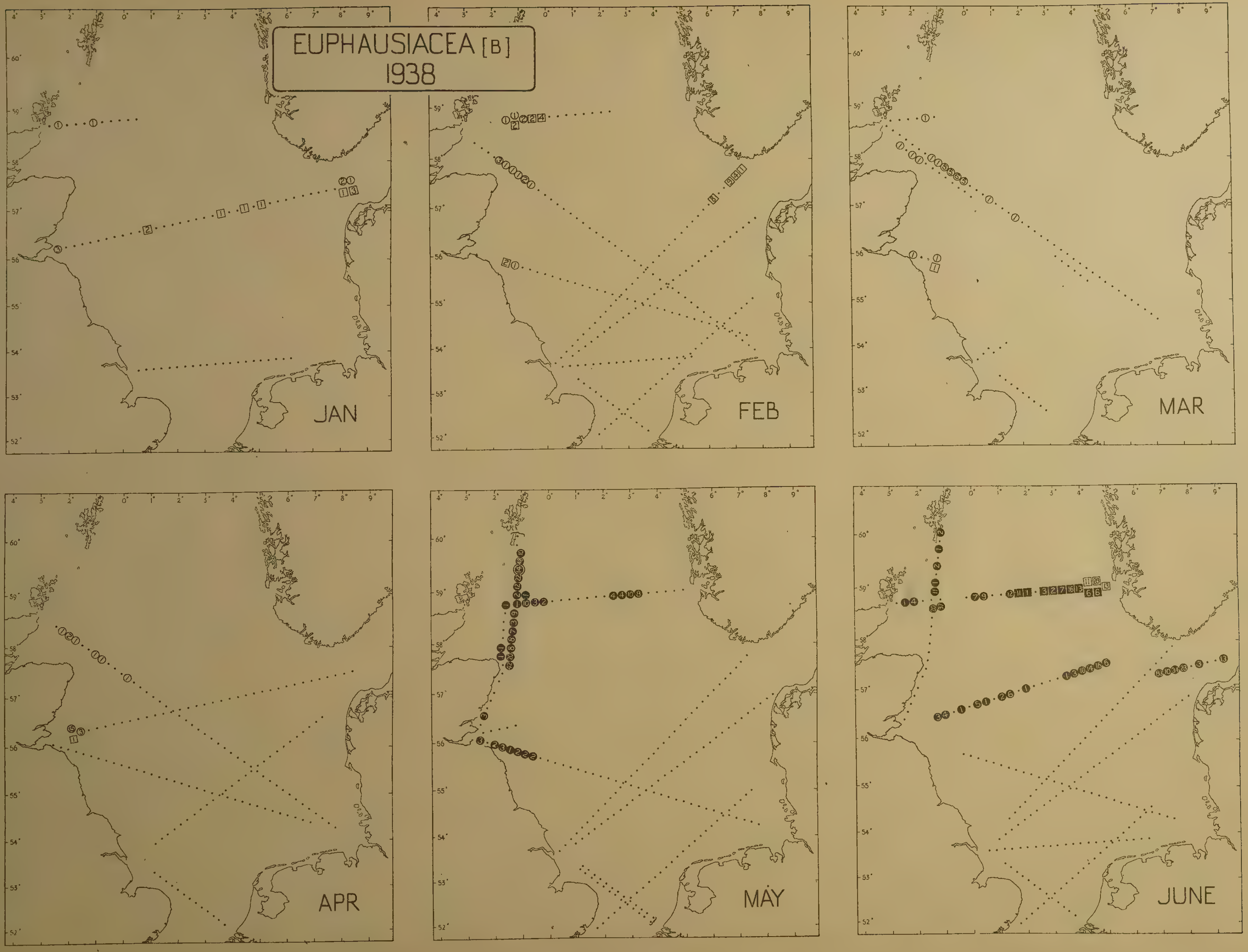

AUG
SAGITTA
ELEGANS SETOSA
PER BLOCK
· : 0
⊕ : 1-9
⊕ : X10
◎ : X100.

PLATE XCVIII



EUPHAUSIACEA [B]
1938

JAN
FEB
MAR
APR
MAY
JUNE

PLATE XCIX

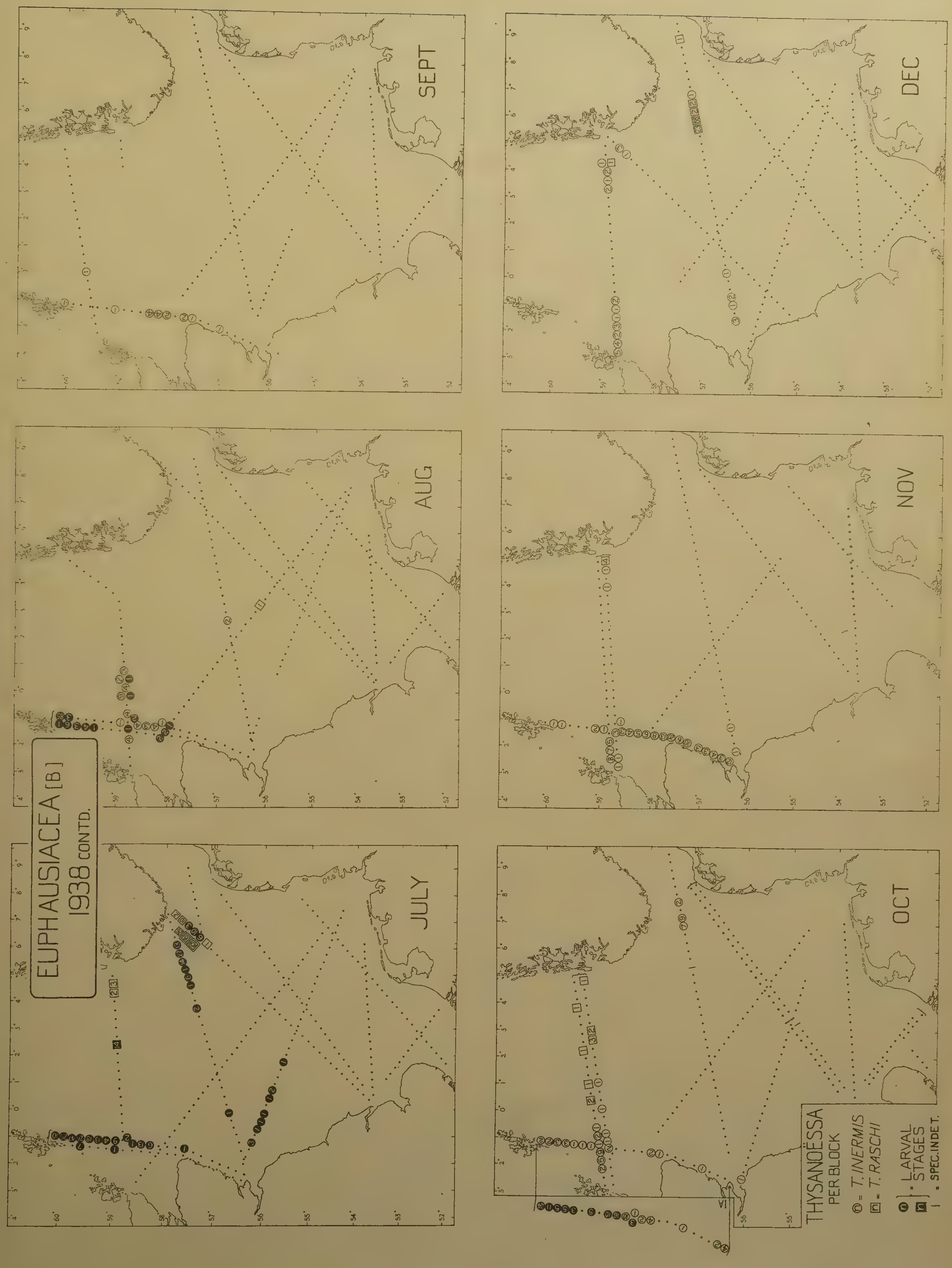

EUPHAUSIACEA [B]
1938 CONTD.
JULY
AUG
SEPT
OCT
NOV
DEC
THYSANOËSSA
PER BLOCK
○ = T. INERMIS
□ = T. RASCHI
● ■ LARVAL STAGES
I = SPEC. INDET.

PLATE C

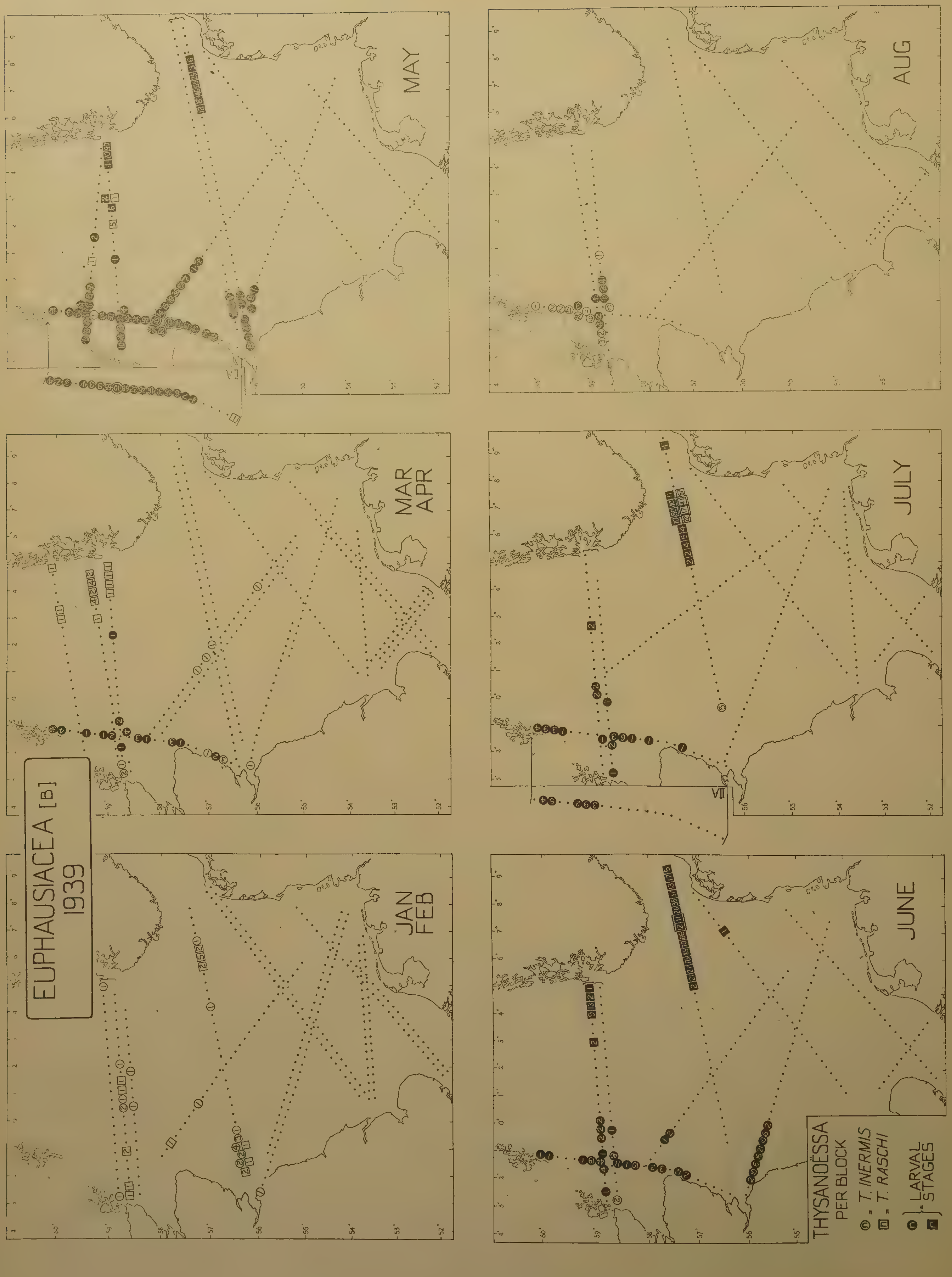

EUPHAUSIACEA [B]
1939
JAN
FEB
MAR
APR
MAY
JUNE
JULY
AUG
VII
IV
THYSANOËSSA
PER BLOCK
ⓘ = T. INERMIS
▣ = T. RASCHI
● ■ = LARVAL STAGES

PLATE CI

LAMELLIBRANCH LARVAE

• - 0
+ - 1-10
∘ - 11-25
○ - 26-50
⊕ - 51-100
◐ - 101-250
● - 251-500

PER MILE PER BLOCK

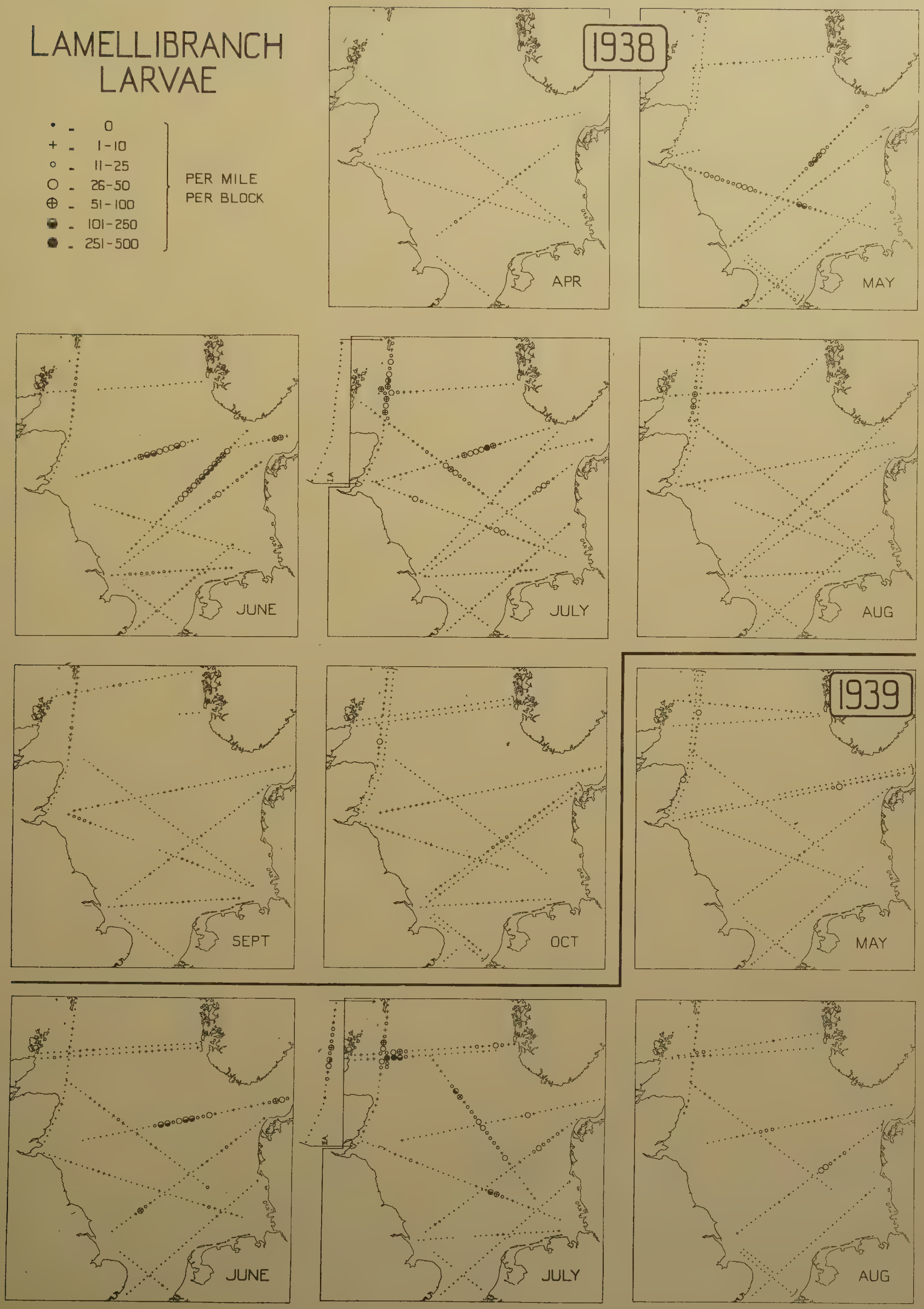

1938
APR
MAY
JUNE
VIA
JULY
AUG
SEPT
OCT
1939
MAY
JUNE
VIA
JULY
AUG

PLATE CII

PODON SPP.

- • = 0
- + = 1-10
- ○ = 11-25
- ◯ = 26-50
- ⊕ = 51-100
- ◒ = 101-250

PER MILE PER BLOCK

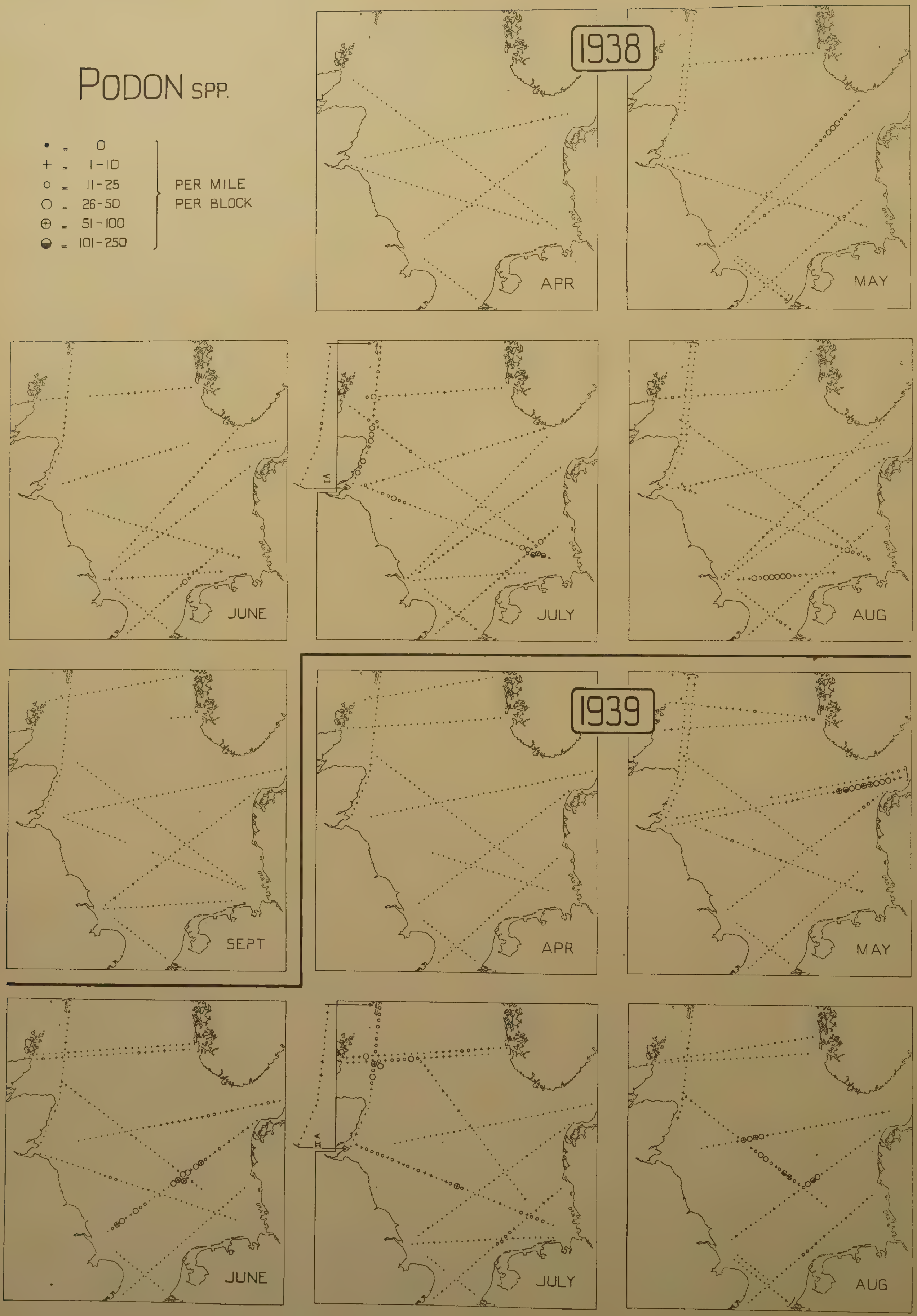
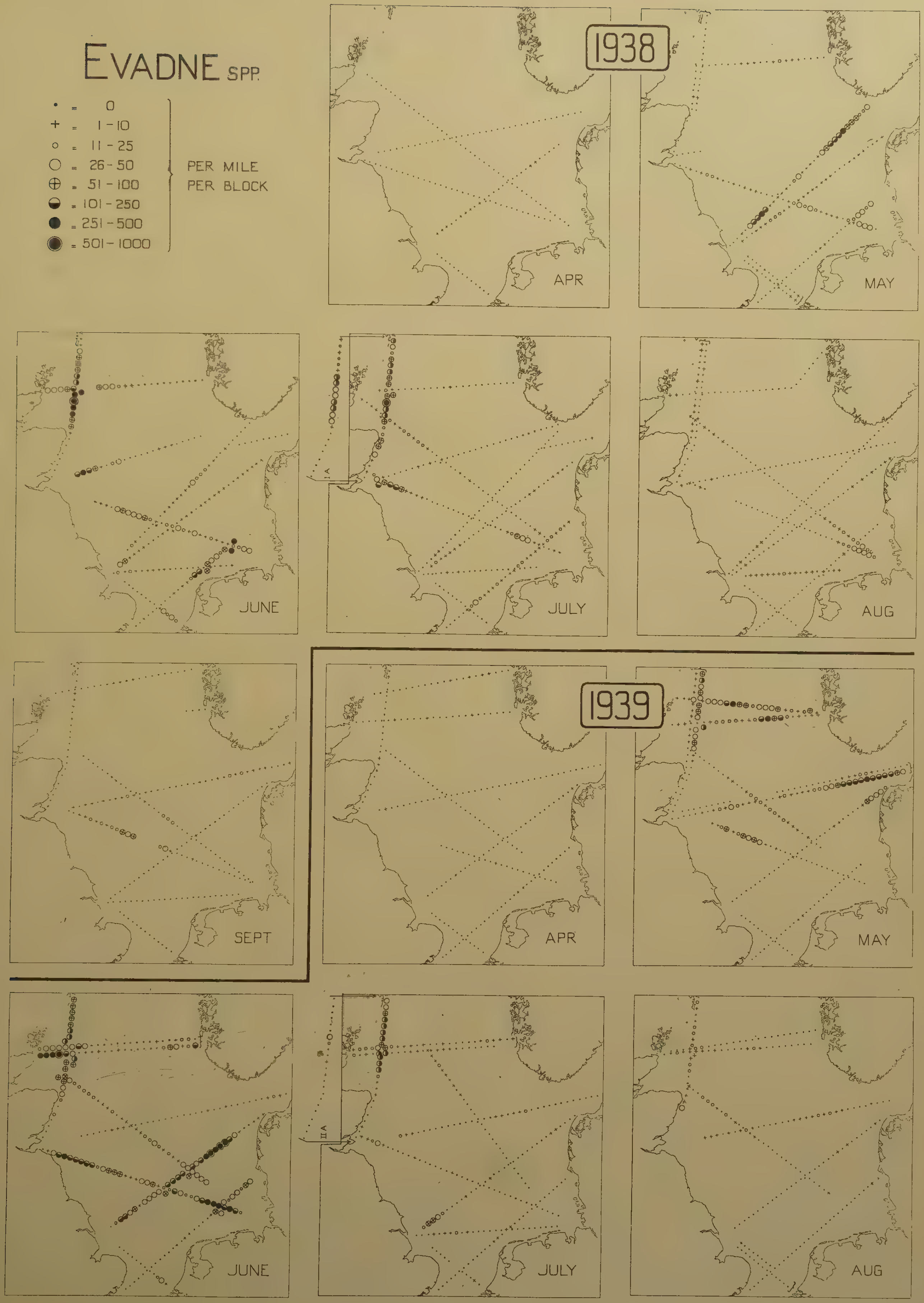

1938
APR
MAY
JUNE
IA
JULY
AUG
SEPT
1939
APR
MAY
JUNE
IIA
JULY
AUG

PLATE CIII

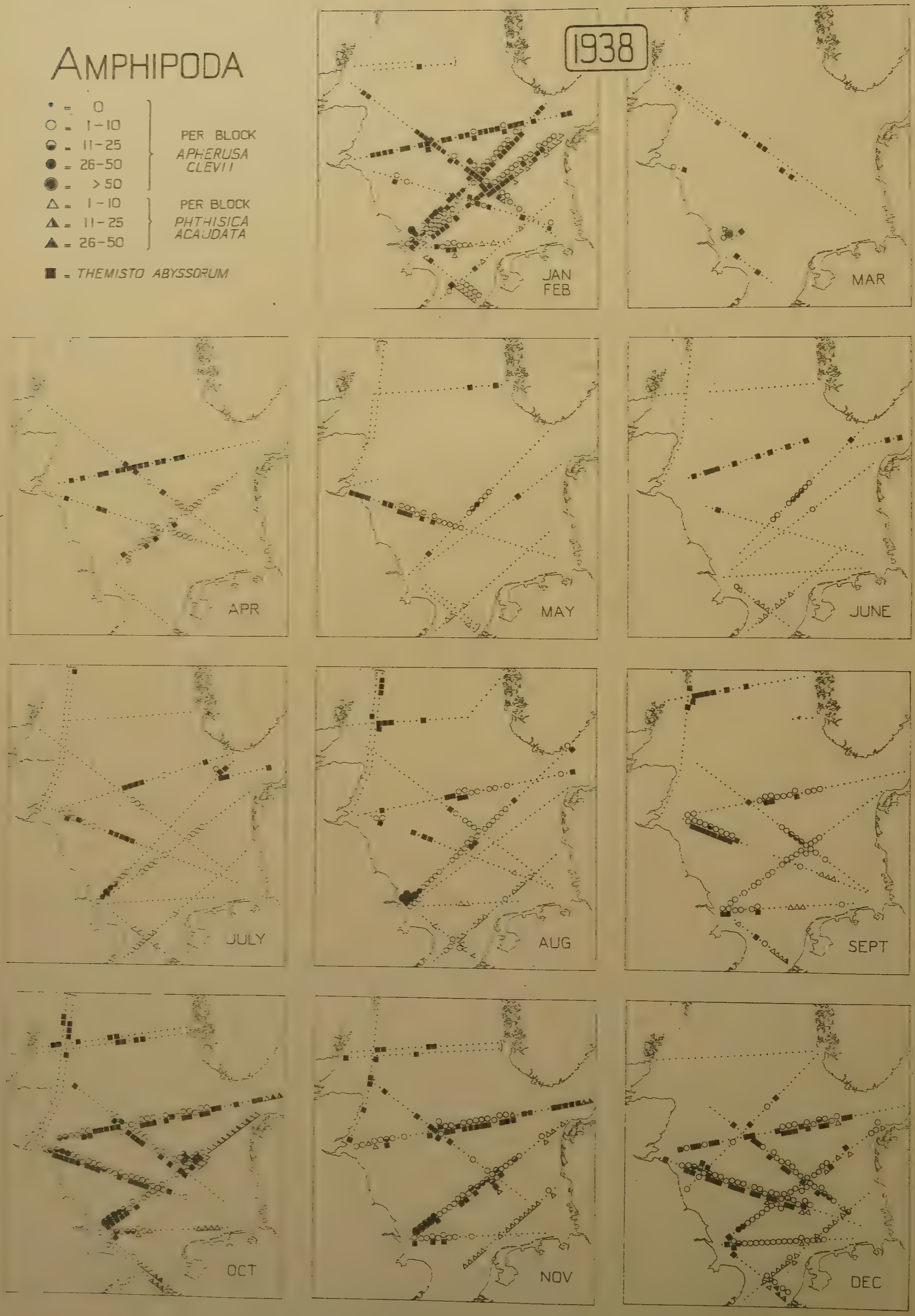


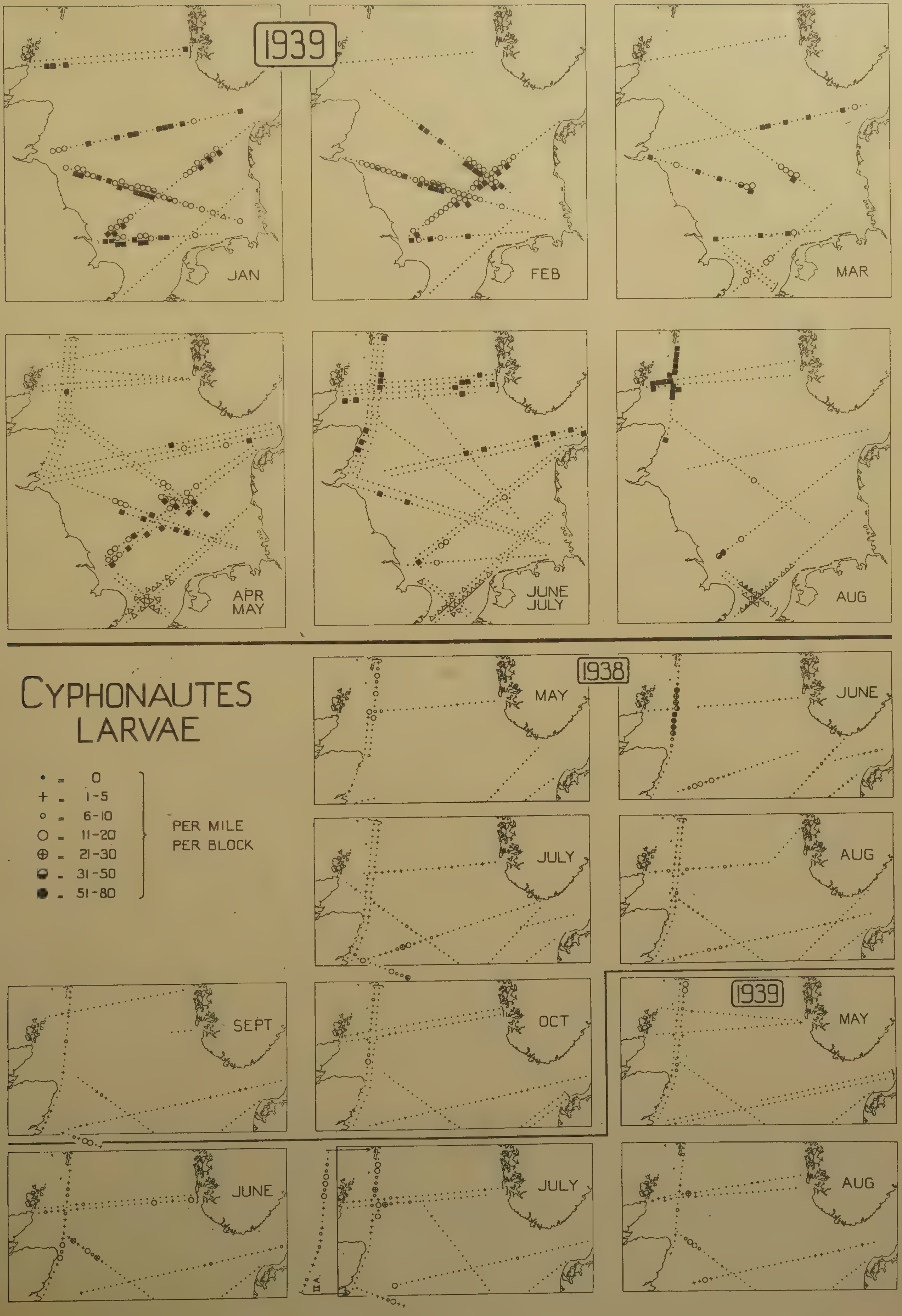
EVADNE spp.

• = 0
+ = 1 - 10
∘ = 11 - 25
○ = 26 - 50
⊕ = 51 - 100
◒ = 101 - 250
● = 251 - 500
◉ = 501 - 1000
PER MILE
PER BLOCK
1938
APR
MAY
JUNE
I A
JULY
AUG
SEPT
1939
APR
MAY
JUNE
II A
JULY
AUG

PLATE CIV

AMPHIPODA

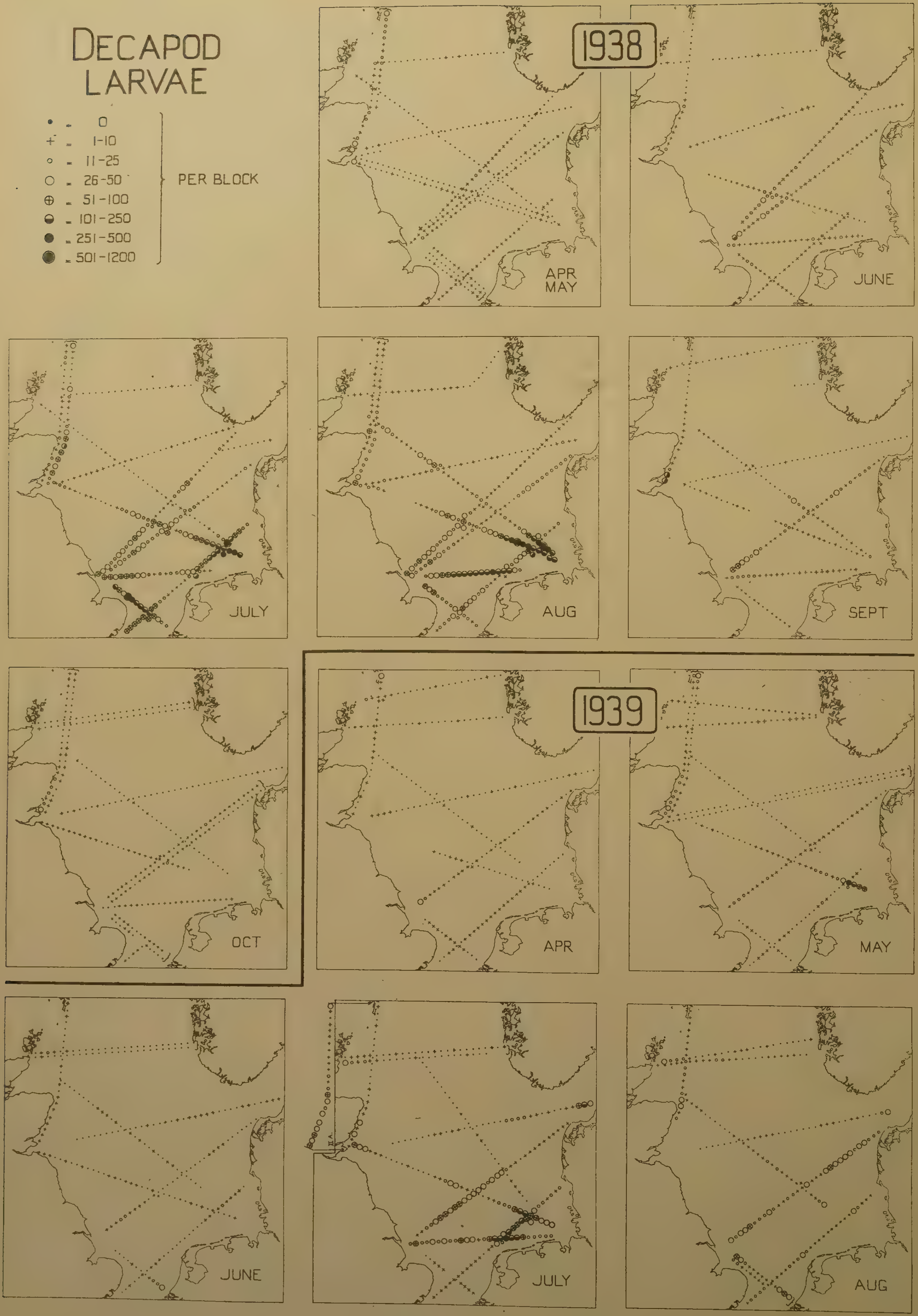

• = 0
○ = 1–10
◒ = 11–25
● = 26–50
◉ = >50
PER BLOCK
APHERUSA CLEVII
△ = 1–10
◭ = 11–25
▲ = 26–50
PER BLOCK
PHTHISICA ACAUDATA
■ = THEMISTO ABYSSORUM
1938
JAN FEB
MAR
APR
MAY
JUNE
JULY
AUG
SEPT
OCT
NOV
DEC


1939
JAN
FEB
MAR
APR MAY
JUNE JULY
AUG
1938
MAY
JUNE
JULY
AUG
SEPT
OCT
1939
MAY
JUNE
JULY
AUG
IIA
• = 0
+ - 1-5
○ = 6-10
◯ - 11-20
⊕ - 21-30
◒ - 31-50
● - 51-80
PER MILE
PER BLOCK

CYPHONAUTES LARVAE

PLATE CVI

DECAPOD LARVAE


• = 0
+ = 1-10
∘ = 11-25
○ = 26-50
⊕ = 51-100
◒ = 101-250
● = 251-500
⬤ = 501-1200
PER BLOCK
1938
APR MAY
JUNE
JULY
AUG
SEPT
OCT
1939
APR
MAY
JUNE
JULY
AUG

ECHINODERM LARVAE

PER MILE PER BLOCK

- • = 0
- + = 1-25
- ∘ = 26-50
- ○ = 51-100
- ⊕ = 101-250
- ◒ = 251-500
- ● = 501-1500
- ◉ = >1500

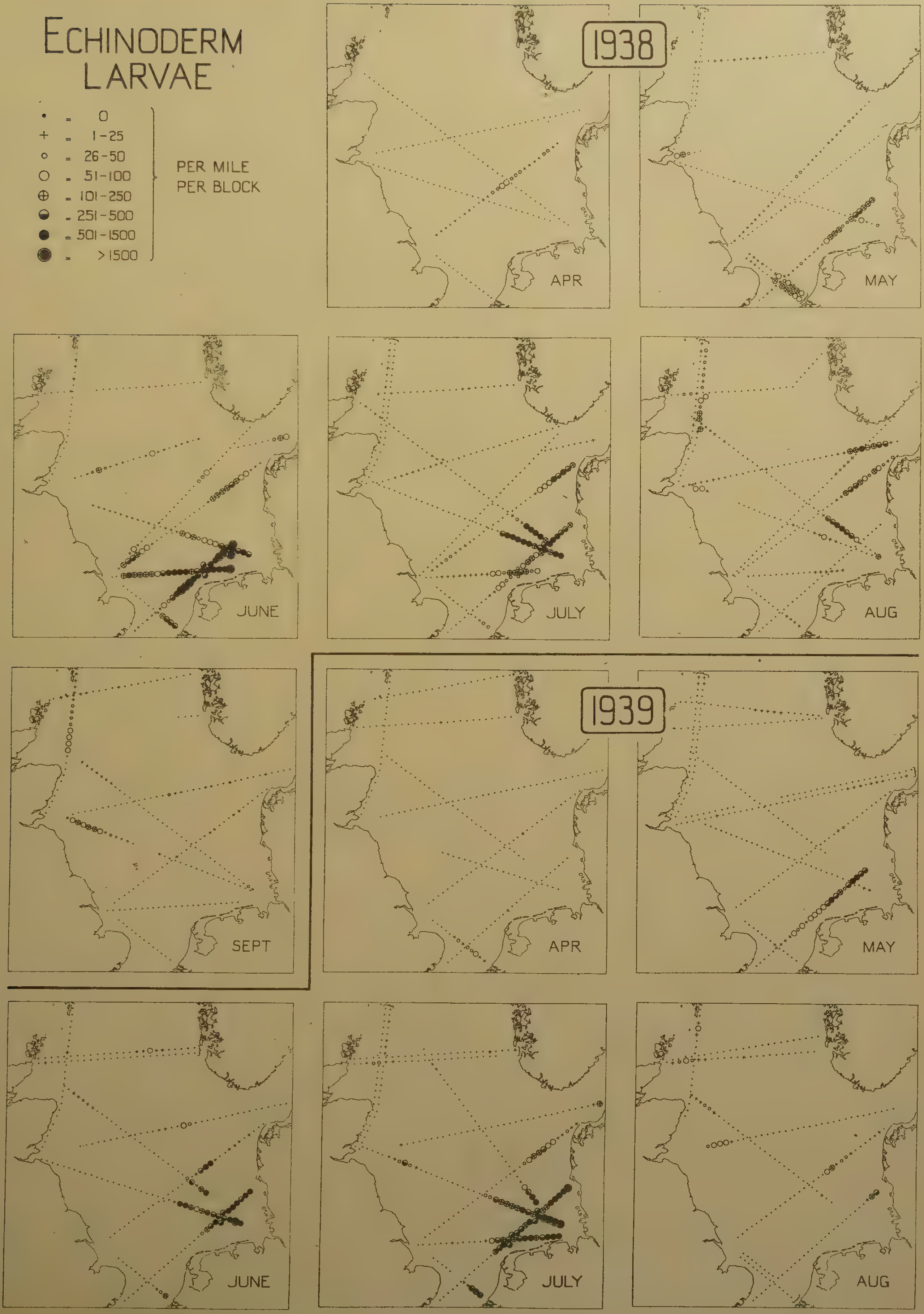
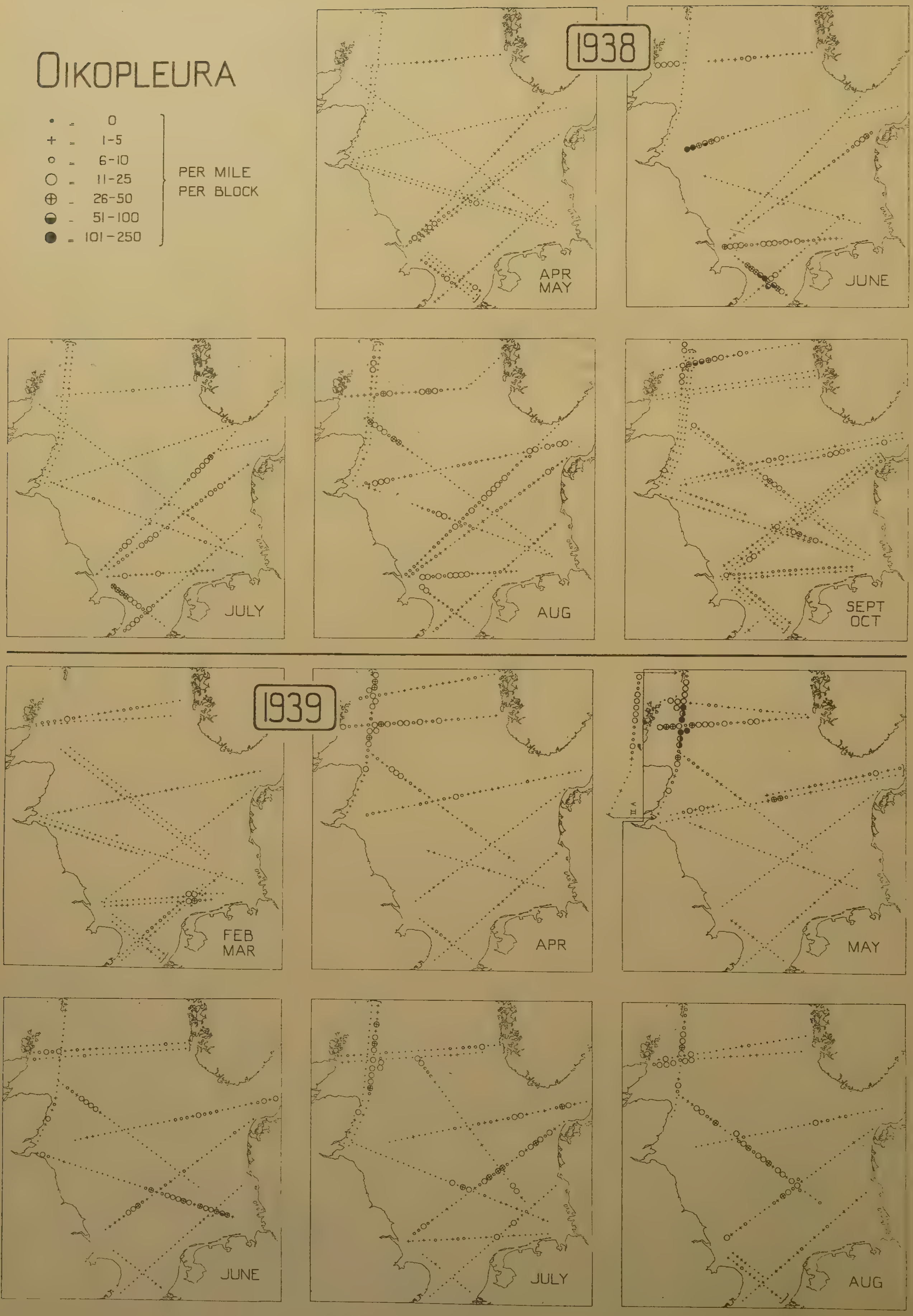

1938
APR
MAY
JUNE
JULY
AUG
SEPT
1939
APR
MAY
JUNE
JULY
AUG

PLATE CVIII

OIKOPLEURA

• =	0
+ =	1-5
∘ =	6-10
○ =	11-25
⊕ =	26-50
◒ =	51-100
● =	101-250

PER MILE PER BLOCK


1938
APR MAY
JUNE
JULY
AUG
SEPT OCT
1939
FEB MAR
APR
II A
MAY
JUNE
JULY
AUG

[*Hull Bulletins of Marine Ecology, No. 14, Vol. II, pp.* 215–275, *September, 1949.*]

CONTINUOUS PLANKTON RECORDS:

THE DISTRIBUTION OF *CALANUS FINMARCHICUS* (GUNN.) AND ITS TWO FORMS IN THE NORTH SEA, 1938-39.

BY

C. B. REES, M.Sc.

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DISTRIBUTION OF CALANUS IN THE SOUTHERN NORTH SEA, 1932–39 . 270

INTRODUCTION, MATERIAL AND METHODS.

In 1932–37 the plankton recorder survey covered only the southern North Sea. Calanus was taken in much lower numbers than many other copepods and was separated only into "large" and "small" stages; Rae and Fraser who reported on the Copepoda (1941, 'Bulletin' No. 4) decided to reserve the Calanus data for a later and more comprehensive study. In January, 1938, the survey was extended to the northern North Sea (Hardy, 1941, 'Bulletin' No. 7), where

Calanus was obtained in much greater quantity ; it was then decided to make a study of its distribution, life-history and size, and the inter-relations of these with water movements.

At a late stage in this study it was found possible to distinguish among the forms hitherto regarded as *Calanus finmarchicus* (Gunn.) two quite distinct kinds which, if they have specific rank, appear to correspond with *Calanus finmarchicus* (Gunn.) and *C. helgolandicus* (Claus). The status of these two, however, has been disputed by some systematists, and the majority of ecologists do not distinguish them. In the present work our two forms have been separated in copepodid Stage IV to adults, and in some measure dealt with independently. Their status and the relations between them will be discussed on p. 264. For the present one form will be referred to as " finmarchicus " and the other as " helgolandicus." When both forms are considered together, *e. g.* in the young stages, the generic name (Calanus)[1] will be used.

The value of continuous recording for studying distribution has been shown in a number of 'Hull Bulletins'. It can conveniently provide samples at regular time intervals over a very wide area under standard conditions, so that the data can be compared *inter se* month by month and year by year. It is recognized that a record at a single depth of 10 m. is subject to the limitation imposed by the changing vertical distribution, both seasonal and diurnal, of such an animal as Calanus. It may be said now, however, that a close analysis of the available Calanus records has failed to show any marked effect which might be due to diurnal vertical migration (p. 218), although this is not to say that such vertical migration does not occur, or even that it does not affect the recorder material. On the other hand there is, taking into account the results of other workers, some evidence of a seasonal migration, more particularly in February and March, and certain other features in the data may also be due to this.

During routine analysis, and before sub-division into the two forms, Calanus as a whole was separated into males, females, Stage V, Stage IV, and " young stages " (copepodid Stages I–III combined). The fact that records were commonly taken at rather long intervals, compared with the rate of development of Calanus, makes it probable that there was no great loss of information in combining the early stages. No attempt was made to estimate eggs and nauplii.

Young stages were analysed in the same way as other small and common copepods (Rae and Rees, 1947, p. 96). Stage V and adults, up to a total of ca. 100 on each 10-mile unit of silk, were counted with the unaided eye. When more were present, not less than one twentieth of the silk was examined microscopically, and an estimate obtained of the number on the 10-mile unit. A proportion of all the large Calanus present was then assessed as males, females, and Stage V copepodites. Stage IV, being intermediate between young stages and Stage V in frequency and size, was either sub-sampled or counted directly according to circumstances.

---

[1] An account of the small number of *C. hyperboreus* recorded has been given by Rae and Rees (1947).

The monthly distributions along the recorder lines of Stage V and adults combined, and of Stages I–IV combined, are shown in Plates LXXIV–LXXVII and LXXXV of 'Bulletin' No. 11 (Rae and Rees, 1947) and briefly described. It is regretted that these plates cannot be reproduced in the present paper owing to the cost of printing.

In dealing with other copepods it was found useful for certain purposes to divide the North Sea into arbitrarily chosen areas, A, B, C, etc. (Rae and Rees, 1947). The chart used on Text-fig. 2 of this paper shows the boundaries of these areas. For each of them the average numbers of Calanus per 10-mile unit per month have been calculated to provide the data shown in Text-fig. 2 which is directly comparable with the corresponding figures for Total Copepoda, Temora, etc., given by Rae and Rees.

The sizes of the metasome of some 2500 females and 6700 Stage V copepodites were measured with a micrometer eyepiece (unit = 0·032 mm.). Groups of such measurements (ranging from 6 to over 200), from the appropriate parts of any record occurring within the limits of an area, have been used to give an average size for that area for the date of that particular record. Altogether about 150 averages of Stage V and 100 averages of female sizes have been determined.

When the two forms were distinguished in later measurements, it became clear that, for at least a large part of the year, their average sizes were markedly different (Text-fig. 15). Since their relative numbers varied with time and place, it is not always possible to distinguish in the original Calanus measurements the effect of a true seasonal change in size from that of a change in the proportion of the two forms. However, from their known distribution it appeared that in many cases only one, or mainly one, form had been present when measuring the whole group of Calanus. Such a group average size has been adopted as representative of one form only when it is unlikely that more than 10% of the other form were in the population. In other cases[1] the Stage V population has been split into the two forms and the average size found for each. Such "split" populations are clearly indicated.

Only a selection of the data can be presented here, but the complete data of size measurements are filed for reference in the Oceanographic, Laboratory, Leith.

The data for the whole North Sea, 1938–39, are considered in the main report, this being a companion to that on the other Copepoda for this period (Rae and Rees, 1947); an appendix provides a brief account of the seasonal changes in Calanus from 1932 to 1939 in the southern North Sea only.

---

[1] The average sizes of Calanus populations suspected of including more than 10% of another form mixed with the dominant one have not been used in this report. Thus, most of the group averages obtained during the first half of the year, when "finmarchicus" was outstandingly dominant, have been accepted, but few in the latter part when the two were generally more equally mixed.

LIMITATIONS.

The purpose of the recorder is to obtain a general picture of the plankton, and compromise has been essential. Limitations have thus been placed on the Calanus collection which might have been avoided had Calanus been the chief objective of the survey.

In general the use of 60 mesh silk is suitable for the collection of those stages estimated. The openings between the meshes of wet silk are about 0·2 mm. across, whilst the diameter of Stage I with appendages pressed close to the body is about 0·25 mm., and of Stage II 0·3–0·4 mm. (Farran, 1927).

It is not likely that the small opening of the recorder ($\frac{1}{2}$ in. square) allows more than a very few even of the late stages to evade capture. Gran (1900) and Farran (1927) refer to the possibility of escape from nets, Gardiner (1933) from plankton indicators, and Clarke and Zinn (1937) from collecting pumps. The recorder, however, is towed at relatively high speeds, from 9–15 knots, which must make it much more difficult for an individual to avoid capture.

It is the fact that the recorder collects samples at a constant depth of 10 m. which places the most formidable limitation on the present data. That the vertical distribution of Calanus varies seasonally and diurnally has been shown by a number of workers, including Russell (1928) at Plymouth, Gardiner (1933) in the North Sea, Nicholls (1933) in the Clyde Sea area, Farran (1947) off Ireland, and Clarke (1933) in deep Atlantic water. The conditions determining the varying distributions would appear to be most complex, as the experimental work of Hardy and Paton (1947) indicates, and results certainly appear to differ according to the local conditions.

Marshall (1948), dealing with Euphausians, shows how marked may be the influence of diurnal migration on recorder collections, but analysis of the Calanus records failed to show any such obvious effect. Marked changes in the total numbers of late stages along the records occurred independently of time of day, and marked changes in the relative proportions of the two forms were also independent. It has not been possible to show that, overall, collections were larger at any one part of the day relative to sunset and sunrise than at any other part. Hardy (1939), considering the theoretical average vertical distribution of Calanus in the Plymouth area, maintained that in local waters the 10 m. path of the recorder should give the most consistent results throughout the 24 hours. This is further borne out by the appropriate manipulation of data provided by Savage (1931). Thus, Rae and Fraser (1941, p. 181) considered his data for Pseudocalanus, etc., in order to find out how far a haul at 10 m. may be considered representative of the mean density of population over all depths. Their method has now been applied to Calanus and it appears that the 10 m. haul can very usefully represent the overall density. Again, when Savage's stations are split into day and night groups, there is no significant difference between the two groups. Whilst it cannot be denied that diurnal migration probably affected the recorder collections to some extent, the influence was certainly not obvious. Since, in the following account, the average numbers of individuals on groups of *several* 10-mile blocks are commonly used, the effect of diurnal migration must be further minimized because of the time span in recording over such distances.

It would appear, therefore, that spatial and seasonal changes in numbers along the records at depths of 10 m. were generally greater than the usual changes imposed by diurnal and vertical distribution.

Of seasonal changes in distribution, it can only be said that, apart from the probable upwards migration of the deep over-wintering stock in February–March (p. 244), the data that follow appear to be interpretable in terms of life-history and water movements, without invoking explanations based on seasonal changes in depth. Again, however, it does not follow that such changes did not occur.

Differentiation of the Two Forms of Calanus.

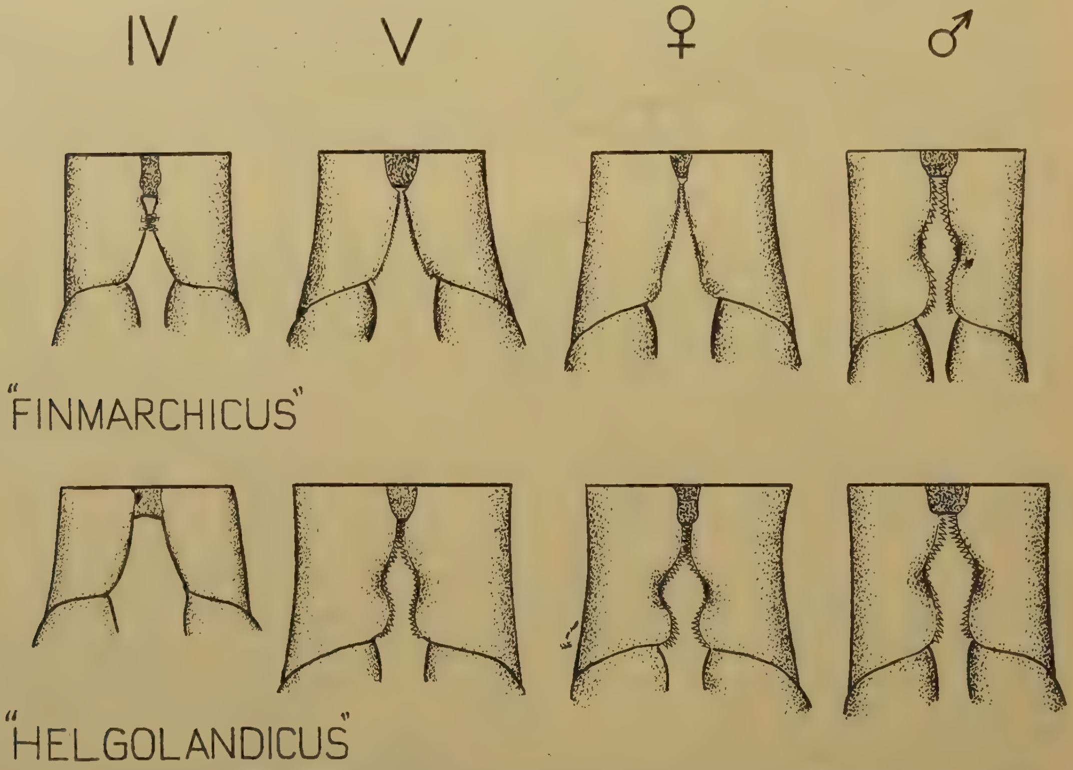
At an early stage in this work attempts were made to separate *Calanus finmarchicus* (Gunn.) from *C. helgolandicus* (Claus). Owing to the somewhat crushed state of the zooplankton collected by the recorder, it is seldom possible to effect such a separation satisfactorily in accordance with the characteristics given, for instance, by Sars (1903), although usually such separation is possible with tow-net samples. Even then, most, if not all, of the characters used by Sars are probably variable, so that doubt may frequently arise as to the correct placing of an individual (*cf.* p. 264).

Little further knowledge of these two forms has been gained since With (1915) pleaded for a more thorough investigation and a final decision as to their status. Whilst some systematists are of the opinion that there are two distinct species (*e.g.* Sars, 1903, Wilson, 1932, and Rose, 1933), others would appear to imply that *C. helgolandicus* should not be recognized as distinct from *C. finmarchicus* (Wolfenden, 1904, and With, 1915). Furthermore, most ecologists either believe that there is only one species, or find the difficulties of separation too great, so that records of *C. finmarchicus* far outweigh records of *C. helgolandicus*. Again, there is not complete agreement on the detailed structure of the two forms, even among those who believe that they are distinct species.

Towards the end of the present work, it was found possible to divide the material hitherto termed *C. finmarchicus* into two forms according to the structure of the first basipods of the 5th legs. In general, the evidence suggests that it is appropriate to call these two forms by the names " finmarchicus " and " helgolandicus."

In the form " finmarchicus " a line of teeth runs along the inner margin of the first basipod segment of the 5th legs in Stage V and females and, in appearance, varies from slightly convex to slightly concave (Text-fig. 1). This agrees with Sars' drawing of *C. finmarchicus*.

In Stage V and females of the form " helgolandicus," this tooth line does not follow the inner margin of the basipod but curves in the centre part of its run towards the posterior side of the segment and is, in appearance, strongly concave (Text-fig. 1). In this, but unlike Stage V and female " finmarchicus," there is a close similarity to the males of both. Because of the way the tooth line curves in " helgolandicus " it is quite possible to observe one leg in such a way that it looks like a " finmarchicus " leg, but it is never possible for both legs of an attached pair to look from the same viewpoint like " finmarchicus " legs.



Text-fig. 1.—Tracings of photomicrographs of the basal joints of the fifth pair of thoracic appendages of the forms " finmarchicus " and " helgolandicus " of Calanus.

Claus (1863) first described *C. helgolandicus* (as *Cetochilus helgolandicus*) and drew the female 5th leg with a concave tooth line. It is not a good drawing but the concavity as shown is much more pronounced than the occasional slight concavity in the appearance of " finmarchicus " legs.

According to Sars (1903), Giesbrecht (1892) used the name *C. finmarchicus* as a synonym for *C. helgolandicus* (Claus). Reference to Giesbrecht's monograph shows that the degree of asymmetry in his drawing of the 5th leg of the male (his Plate 8, fig. 31) confirms his species as the *C. helgolandicus* of Sars, whilst the drawing of the 5th leg of the female (his plate 8, figs. 20 and 21) is exactly that of the " helgolandicus " character used in the present survey. Giesbrecht's description is also exact : " . . . bei *finmarchicus* (*helgolandicus*)[1] mit einem gezähnelten Saum am Innenrande ; derselbe ist bei *finmarchicus* (*helgolandicus*)[1] in der Mitte concav und nach der vorderen Gliedfläche zu aufgebogen."

It is possible to pick out from a tow-netting females which are typically *C. finmarchicus* and *C. helgolandicus* by following Sars' (1903) descriptions. In every case when this has been done the 5th legs were found to be as shown in Text-fig. 1, *i.e.* those here termed " finmarchicus " and " helgolandicus." With a little experience it is possible to separate those individuals having the two types of leg in any net collection with very few errors by examining only the shape of the frontal margin, this being one of the specific characters given by Sars. In the course of separating several thousands of females and Stage V by this character of the 5th leg, there never arose any doubt as to the category of any individual.

Only about 100 males were identified in the recorder material. Separation of the two species *C. helgolandicus* and *C. finmarchicus* according to the degree of asymmetry of the 5th legs, following Sars' account, presented no difficulty, and it was found that the geographical distribution of the males of the two species was such that the male *C. helgolandicus*, for instance, occupied the area occupied by the Stage V of " helgolandicus " (p. 226). Further, the North Sea distribution, both seasonally and geographically, of females of the two is such that, when compared with the males which have been separated on Sars' description, there is again little reason to doubt that our variety " finmarchicus " corresponds with *C. finmarchicus* (Gunn.) and " helgolandicus " with *C. helgolandicus* (Claus).

For all that, there was hesitation before deciding that the structure of the basipod does delimit precisely two forms " finmarchicus " and " helgolandicus " which correspond with Sars' two species in Stage V and females, since such a careful observer as Sars, as well as many others, has not even referred to this aspect of the structure. Furthermore, it will be seen (Text-fig. 14) that in this work " helgolandicus " has in general been found to be larger than " finmarchicus " (size ranges overlapping), whereas all systematists who accept them seem to have been in agreement that *C. finmarchicus* is the larger of the two species. However, *C. finmarchicus* has a great range of size ; Wilson (1932) gives the range as 2·75–6·5 mm. for females, and in the North Sea we might expect it to be towards the lower end of its size range. Seasonal variation in size is also considerable (Text-fig. 15). As far as the North Sea is concerned Sars' somewhat indefinite statement that *C. helgolandicus* is " rather inferior " in size does not apply.

In the case of Stage IV there is much greater variation, but again there appear to be two typical forms. In the most typical specimens of one, believed to be " finmarchicus," the last basipod segment is stumpy with a distinct " bulge " on the inner margin bearing a bunch of about 12 teeth (Text-fig. 1). There is, however, wide variation in the definition of the bulge, and the number, strength and detailed arrangement of the teeth. In the other, " helgolandicus," the basipod

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[1] Author's insertion bracketed. It is presumed that " nach " means " behind " or " away from " and not " towards " in this context.

segment is not stumpy and has a slightly convex to straight inner margin without teeth (Text-fig. 1). In the more intermediate case the basipod segment may have an indistinct bulge and only 2 or 3 weak teeth. It has been taken in this report that the presence or absence of teeth finally distinguishes the two types. With (1915, Fig. 2) gives a good drawing of the 5th leg of Stage IV *C. finmarchicus* and this corresponds with the present determination of "finmarchicus" IV. In the absence of breeding experiments, it is clearly impossible to *prove* that the Stage IV "finmarchicus" give rise to the corresponding Stage V, and the same with "helgolandicus." Their structure and spatial and seasonal distributions, however, do suggest that this is so.

As regards the status of these two forms, this report presents no final answer, and it is doubtful whether such an answer can be obtained except through difficult breeding experiments under culture. The report shows (1) a close resemblance between the life-history of the two forms, and (2) a regular replacement of one form by the other, according to geographical situation, within the framework of the life-history. These relationships, together with the gradation of some, at least, of the characters assigned by Sars (p. 264), may lead one to think that the two forms here separated, as probably Sars' two species, are truly of one species *C. finmarchicus* (Gunn.). They will be so regarded here, but no important conclusion will be presented which does not also apply should the two forms prove later to be distinct species.

Distribution over the North Sea in 1938–39.

Distribution of Calanus as a whole.

Charts showing the distribution of Calanus had already been printed when it was found that further sub-division was possible. Since these charts concern a conventional ecological group, brief notes on distribution are given below.

The detailed monthly distributions of Stage V and adults combined are given by Rae and Rees (1947) in Plates LXXVI, LXXVII and LXXXV, and of the Stages I–IV combined in Plates LXXIV, LXXV and LXXXV. Unfortunately, a number of records were missed in the early months of 1938 and it is hardly possible to describe adequately the distributions during this period. There was adequate sampling, however, in 1939, and it is best to take this as the standard for the first part of the year. The following notes review some of the chief features of the distribution, which is further summarized in Text-fig. 2 by means of area histograms.

The first significant increase of young stages in 1939 occurred in March, particularly off the Skagerrak. In April numbers generally remained at a low level, except for the west Dogger region and to the north of Bergen. In May there was a great increase north of Lat. 55° 30′ N., contrasting with the decrease in numbers south of this latitude where young stages were almost absent. The northern numbers then decreased and remained relatively scarce until August.

The distribution of late stages corresponds with the sequence in young stages. In April and May high numbers were obtained in several very small patches, except off the Norwegian coast where they were more extensive. In June, following upon the outburst of young stages in May, late stages reached very high numbers right across the North Sea around the latitude of the Firth of Forth. In July high numbers were mainly limited to the north east, and by August there was a general decrease in numbers.

The 1938 sequence of young stages was different. Instead of a great outburst over the northern part in May, extensive coastal patches occurred in succession, off the Norwegian coast at first, and then successively from Shetland to the Firth of Forth. Thus, good numbers were obtained off the Skagerrak in April, off Bergen in May, at the Shetlands in June, and south of Fair Isle and the Forth in July. These young stages were followed by late stages, off the Skagerrak and off Bergen in June, the Shetlands in June and July, and off the north-east coast of Scotland in August. The north-eastern concentrations persisted until July, and those off Shetlands right through to October; but south of Fair Isle numbers had greatly decreased by September and no concentration of late stages occurred off the Forth following the young stages of July.

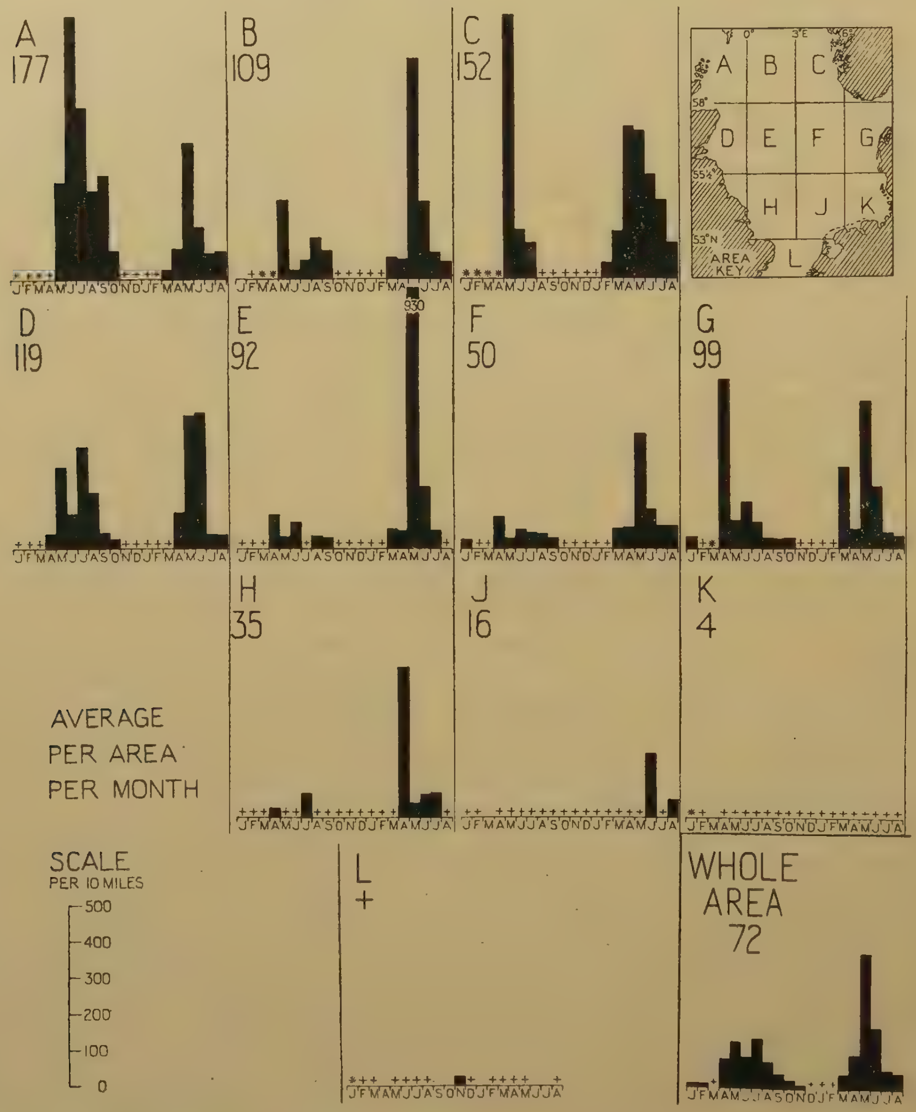
Certain lesser features of the distribution are of interest. In both April and May, 1939, narrow patches of late stages occurred off the Humber, the Firth of Forth, Aberdeen, the Moray Firth and the Orkneys. In addition to these two months, a narrow patch of late stages occurred off the Humber in June and July, 1939. From west to east along the Dogger there were associated patches in 1939, starting with young stages in April, followed by late stages in May, young stages in June, and late stages in July and August. Such a persistent association of patches may be connected with the Dogger Bank swirls in the same way that the persistence of late stages south of the Shetlands until October may be connected with the East Shetland Swirl.

Usually there is a logical association between the distribution of young stages and late stages. The most noticeable dissociation arises from the high number of late stages off the Humber in July 1938, since there appeared to be no sufficient concentration of young stages earlier in the same locality to account for these numbers.

The higher numbers of the north are clearly brought out in Text-fig. 2 which gives the average monthly numbers of the combined Calanus stages per 10-mile unit for each of the areas A–L, and for the whole North Sea. For each is shown under the area letter the average number per unit over the whole 20 months. These numbers are not equally reliable; the absence of records in early 1938, for example, particularly in B and C, affects the results, but it is obvious that the numbers obtained south of latitude 55° 30′ were much the lower (see also Appendix). The most productive area in the south, H, includes the off-Humber and S.W. Dogger Bank and, with an average of 35, it was substantially less populated than the poorest northern area, F. There was a decrease from west to east along the series H, J, K and in areas K and L Calanus was almost absent. Whilst the highest overall average was obtained in area A, this was due to conditions in 1938 rather than in 1939. In 1939 the maximum numbers for A were even less than for E and hardly greater than for F.

Rae and Rees (1947) have already referred to the striking difference between the springs of 1938 and of 1939 in the occurrence of the commoner copepods at 10 m. depth, with maximum numbers in the west in 1938 and in the east in 1939. This, however, is only partially shown by Calanus. In area A, 1938 was certainly the better year, and 1939 in E, F, H and J. In B, C, D and G, however, there seemed no great difference between the two years, although 1939 in D might be considered as a better year than 1938.

One month usually dominated the rest in the production of each area, and

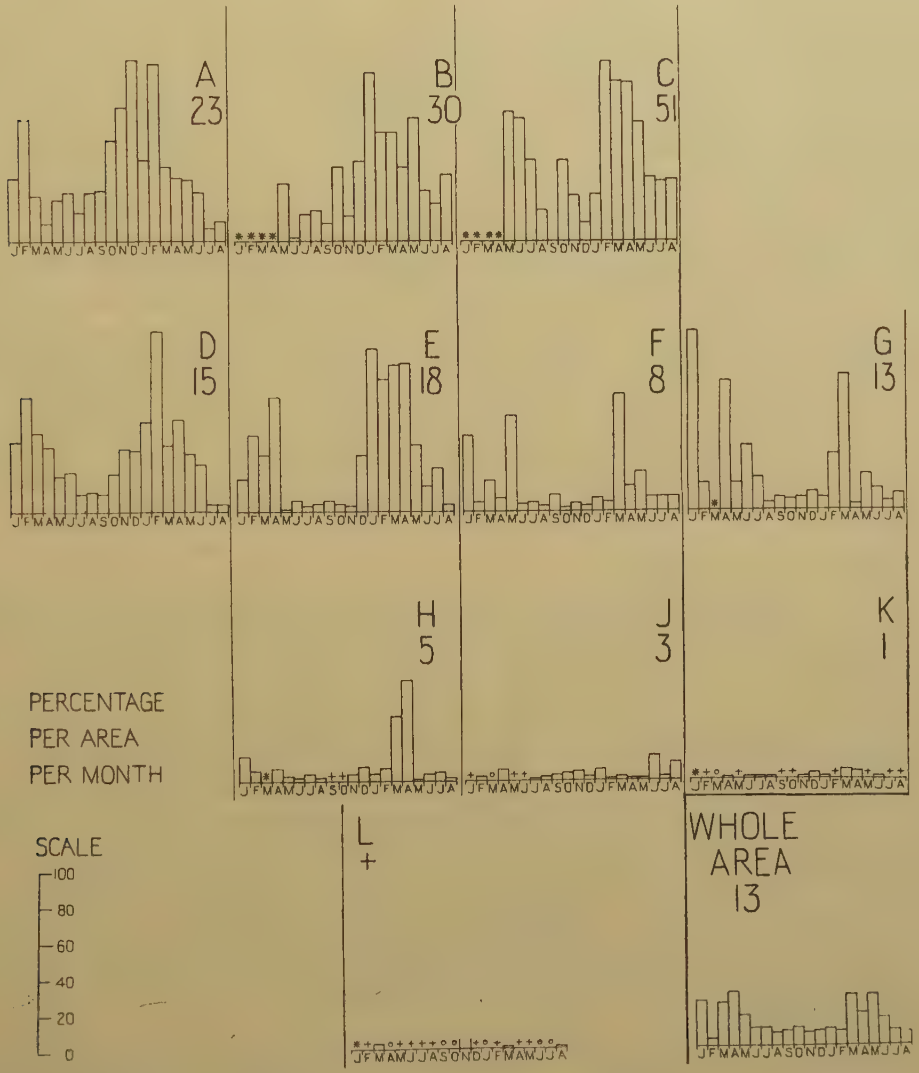


TEXT-FIG. 2 (left).—Histograms (in black) showing the average monthly catch of all stages of Calanus per 10 mile unit for each of areas A–L (see key map), and for the whole North Sea for January, 1938, to August, 1939. (Right).—Histograms (in white) showing the monthly percentage of Calanus in the Total Copepoda for the same areas.

In both sets the values too low to be shown as histograms are shown as +; months with insufficient information to warrant an average are marked ✱. Figures below each area reference letter give the corresponding value for the whole period; similarly for the whole area.

this was most frequently May; consequently this month was the most productive for the area as a whole.

The proportion of Calanus in the total Copepoda decreased from north to south. This is shown in Text-fig. 2, giving the percentage of Calanus in each month and the percentage over the whole 20 months. Only in C was Calanus generally the predominant copepod at 10 m. In all other areas the Pseudocalanus-Paracalanus group (chiefly Pseudocalanus in these waters) was usually predominant. Calanus was the predominant copepod at certain times of the year, however,



Text-fig. 2.—*Continued.*

notably in the winter and early spring. Even so far south as area H, Calanus was predominant in April (in 1939). Later in the year, however, the rate of increase of other copepods combined was greater than the increase in Calanus at the recording level.

Some interesting comparisons may be made between the proportions obtained by the recorder and those obtained by other workers. Gibbons (1933) obtained his material from an area very similar to our area A. In the southern section of his area the percentage of Calanus was at a maximum in May with 76% and a minimum in September with 42%. The average is not far off 50%. For 1938–39 the percentage obtained by the recorder, 23%, was much lower. However, the Annual Report of the Fishery Board for Scotland for 1938 refers to the " unusual abundance of other species of copepods (besides Calanus), especially Pseudocalanus " in 1938 ; also, Gibbons presumably included nauplii in his estimates. Comparison may also be made between area C and Ruud's results off Möre (Ruud, 1929). In 1926 Calanus increased from 15% in March to 63% at the end of April and dropped to 28% in July. The percentages obtained by the recorder for area C were substantially higher, although one might perhaps have expected Calanus to be denser below 10 m. in these deeper waters. Finally, Wimpenny (1933) provides results for his Flamborough Line stations, 48% in February, 25% in March, 9% in August and 2% in October ; month by month these were higher than in area H to the south, and lower than in area E to the north.

Distribution of the two forms.

Further analysis followed the distinction between the two forms of Calanus. Records for the whole North Sea were scanned from July, 1938, to August, 1939 ; then, ten specimens of Stage V and ten females were taken at random from certain suitably spaced 10-mile units and separated into the two forms. Areas were then selected for a consideration of the life histories (p. 231), and in these the Calanus from further 10-mile units were separated until it was judged that the average number of each stage in each area could, with reasonable accuracy, be split into proportionate numbers of the two forms. For this purpose a number of 10-mile units with less than 10 of either stage had also to be analysed, but these separations are not shown in Text-fig. 3. Whilst it is realised that ten or less than ten is a small number in each unit, in all some 1300 Stage IV, 3600 Stage V and 1500 females were " typed," and conclusions are based on the consideration of a number of neighbouring units.

The separation of Stage IV was only undertaken as a means of elucidating breeding, as it is the earliest stage found to be separable into the two types. The analysis was mainly qualitative and what few quantitative data follow can be claimed only to be of the right order. Whilst " finmarchicus " Stage IV was seasonally abundant, " helgolandicus " proved rather rare and the analysis resolved itself in practice into a search for " helgolandicus." In the areas selected for the study of breeding as many Stage IV were separated in each section of a record as the average number of Calanus Stage IV per 10-mile unit in that area on the particular record concerned. Two modifications to this method were introduced: (1) When the average number of Stage IV exceeded 50, no more than 50 were identified; (2) When after the first few identifications "helgolandicus" was found together with "finmarchicus," only sufficient were identified to indicate the proportions of the two species, even though the identified number fell below the average.

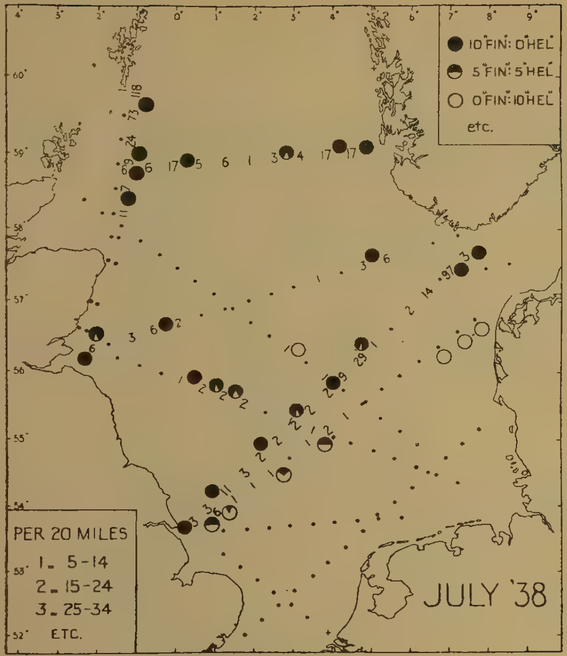
The Stage V "finmarchicus" distribution is shown in Text-fig. 3 (numbers per 20-mile unit) month by month from July, 1938, to August, 1939, excluding February and March. Circles in the monthly charts indicate the forms (wherever sufficient Calanus Stage V were separated), sectors being blacked to represent the proportions of "finmarchicus" in tenths. Thus a fully blacked circle represents an approximately pure "finmarchicus" population and a white circle pure "helgolandicus."

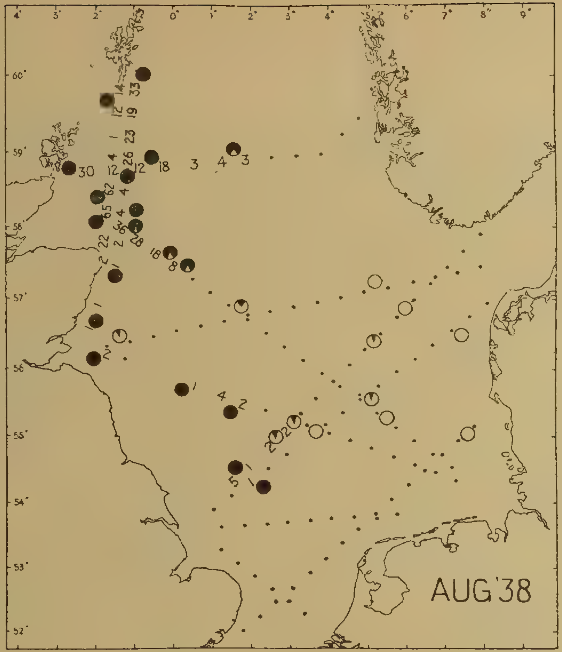
From April to July, 1939, there was at 10 m. a fairly sharp boundary between the dominant "finmarchicus" population to the north and west and the dominant "helgolandicus" population to the south and east. The boundary ran from off the Humber to the north of the Danish coast, mostly north of the Hull-Copenhagen recorder route, except at its Humber end. Separations made in August, 1939, were too few and scattered to determine a definite boundary. July, 1938, was very similar to July, 1939; in August of that year the boundary lay more to the north-west and reached its most northerly position in September. In October there was a marked southward extension of the area of the dominant "finmarchicus" population, covering the Forth area in October–January. South of the Forth Calanus was so scanty during this period that few separations could be made, and these do not show any appreciable change from September to January.

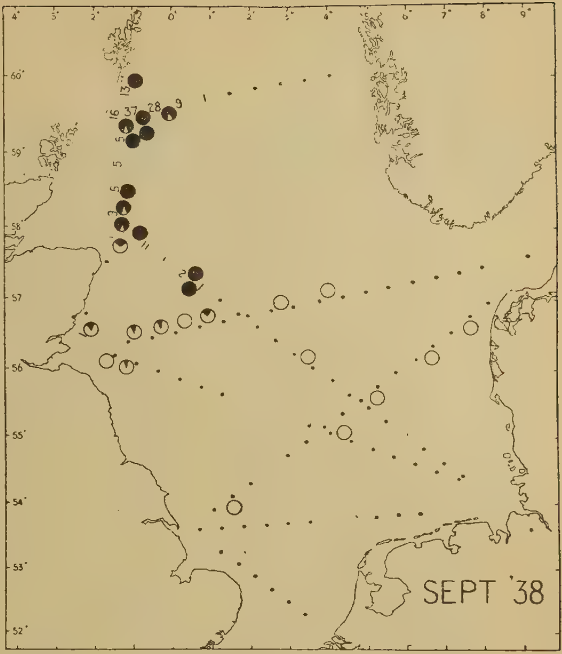
In general, the distribution of the larger numbers of Stage V "finmarchicus" agrees with that of the dominance of "finmarchicus." In particular, high numbers were found only in the north-west in September, 1938, whilst there were very few off the Forth and none off the Humber. In October and November, relatively high numbers were found off the Forth, and in December such numbers extended further towards the east in the same latitude; in the former months very few were taken off the Humber, but in December, for the first time since August numbers had increased slightly.

The extension to the Forth in October suggests that "finmarchicus" V had been transported southwards from its September north-west centre, but this possible movement cannot be satisfactorily followed through November–January in the distributions shown in the figure. Nevertheless, there is a close resemblance between the September and October boundaries of "finmarchicus" V and those of Metridia and Candacia (Rae and Rees, 1947) and Clione (Marshall, 1948). We shall consider later (p. 252), when further information has been given, whether this resemblance is coincidental or whether "finmarchicus" V behaved as an "indicator" of north-western water during this period.

The data for the adults, as well as for Stage IV, of the two forms are much


10 FIN : 0 HEL
5 FIN : 5 HEL
0 FIN : 10 HEL
etc.
PER 20 MILES
1 _ 5-14
2 _ 15-24
3 _ 25-34
ETC.
JULY '38


AUG '38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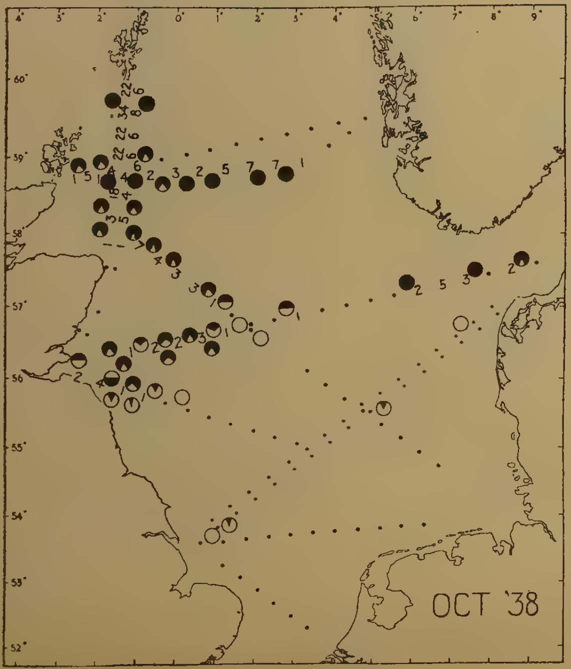
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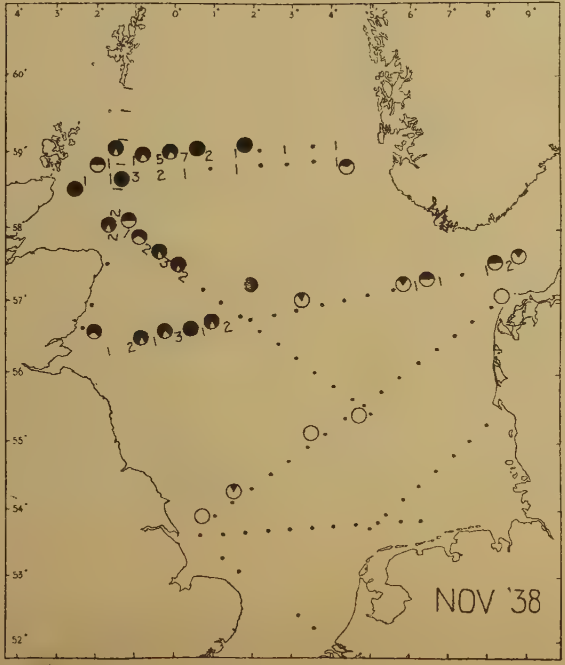
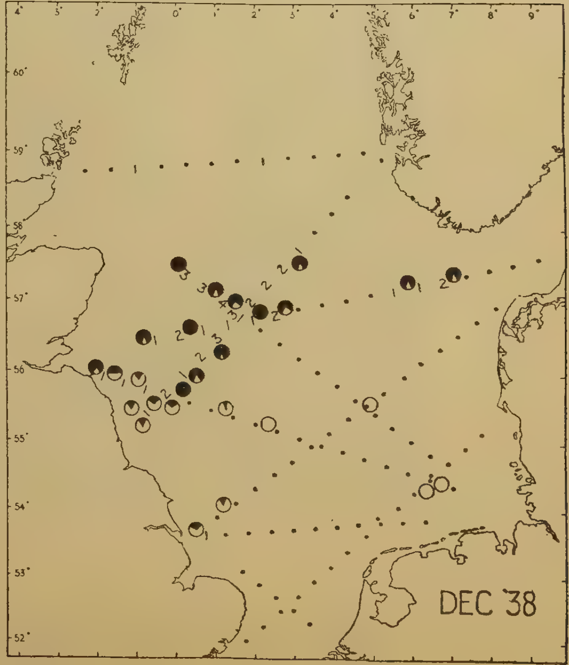

NOV '38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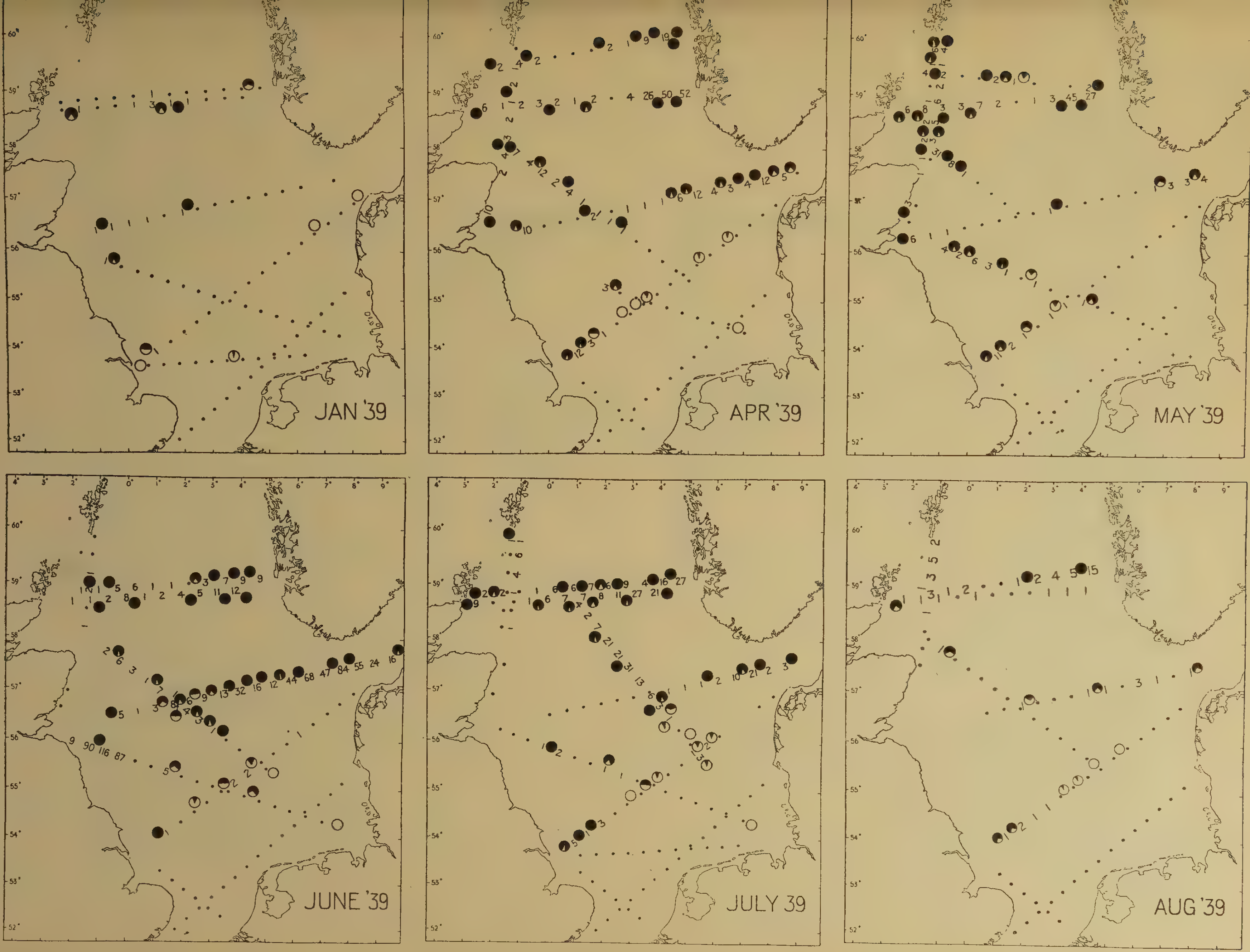
JAN '39
APR '39
MAY '39
JUNE '39
JULY 39
AUG '39
60°
59°
58°
57°
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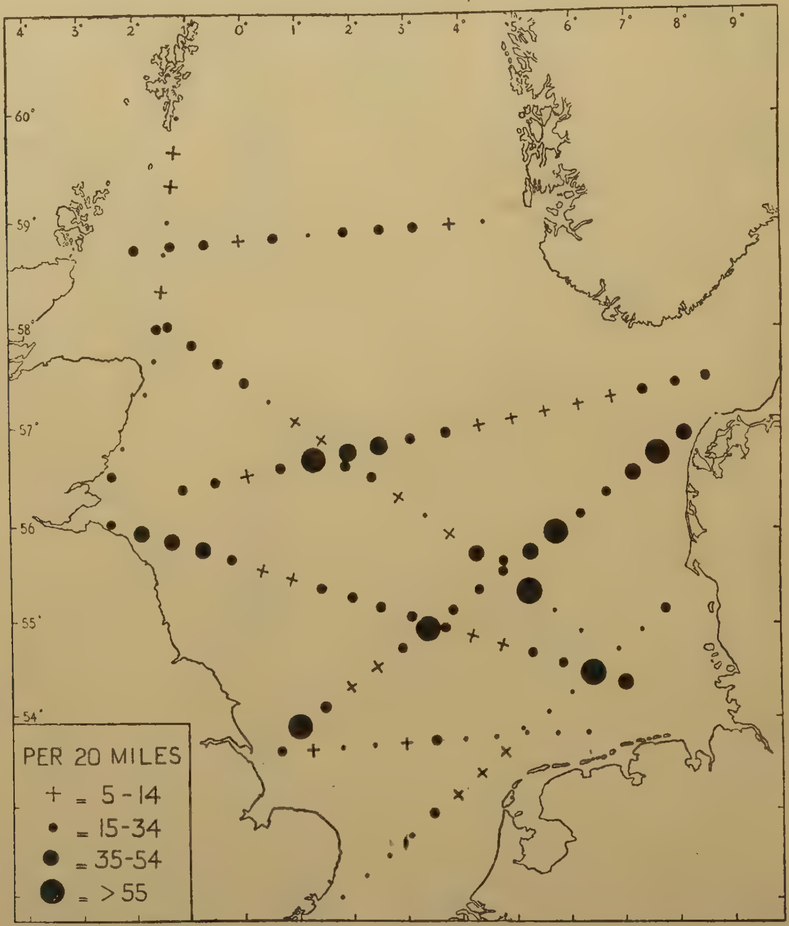
53°
52°
4°
3°
2°
1°
0°
1°
2°
3°
4°
5°
6°
7°
8°
9°

TEXT-FIG. 3.—Charts showing (1) the relative proportions of " finmarchicus " and " helgolandicus " Stage V at various places, sectors of circles being blacked-in to represent the proportion of " finmarchicus " in tenths (see scale); and (2) the numbers of " finmarchicus " Stage V per 20-mile unit (estimated by interpolation, where necessary).

fewer than for Stage V and it is not proposed to review their distribution. It may be said, however, that adult "finmarchicus" did not show such a simple southwards extension through the autumn and winter from a north-western focus, as did Stage V. They could only have done so if the "finmarchicus" Stage V in the autumn and winter moulted quickly to adults which could be collected at a depth of 10 m. Either such moulting did not occur quickly or the resultant adults lived at a depth different from 10 m. (*cf.* p. 250 and Text-fig. 13).

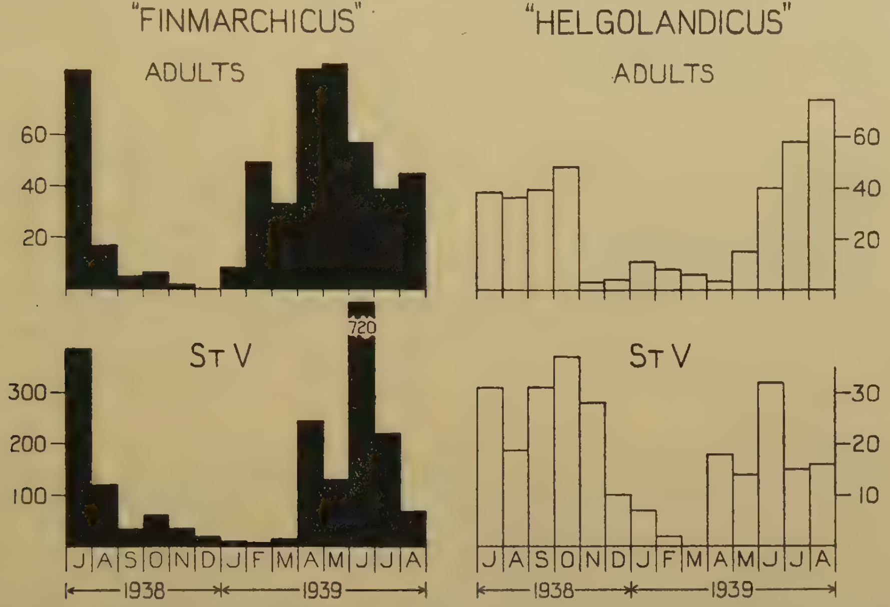


TEXT-FIG. 4.—Chart showing the overall distribution of "helgolandicus" Stage V in the North Sea from July, 1938 to August, 1939. The highest number recorded for each 20-mile unit during this period is represented by a symbol according to the scale.

The overall distribution of "helgolandicus" Stage V is shown in Text-fig. 4, the symbols representing the highest numbers obtained on each 20-mile unit over the period July 1938–August 1939 (*cf.* the method adopted by Rae and Rees, 1947, to show the overall distributions of various species of Copepoda). Of the four types of distribution of Copepoda in the North Sea, defined by Rae and Rees,

" helgolandicus " resembled somewhat that of the central North Sea forms, *Labidocera wollastoni* and *Isias clavipes* ; it was, however, recorded over a much wider range to the north, and especially towards the Forth area. This may possibly be due to its greater abundance in the samples.

The distributions of the two forms in Text-fig. 3 suggest that for the present purpose the groupings of blocks into the areas A–L are not quite satisfactory as a means of summarizing the history of the two populations. The most obvious example is area G, in which are pooled parts of the Leith–Copenhagen and the Hull–Copenhagen lines (Text-fig. 2), although these provided two entirely different populations, the northern one consisting chiefly of " finmarchicus " and the southern almost entirely of " helgolandicus." For the study of the life-histories, therefore, some areas have been further divided, partly to avoid a mixture of populations and partly for simplification. (Thus, area A has been divided because the distribution of young stages near the Shetlands and south of the Orkneys was, in May–July of both years, very different, see p. 222 above and Plates LXXIV–V). The areas selected for study, then, are A(N), A(S), B, C, D(S), E, F(N), G(N), G(S) and H(N), where (N) and (S) mean northern and southern parts respectively. These[1] are shown on the chart inset on Text-fig. 10 and the 10-mile units involved in each area indicated.



TEXT-FIG. 5.—Histograms showing the sum of the mean monthly numbers of " finmarchicus " and " helgolandicus " Stage V and adults of the eight sub-areas A(S) to H(N).

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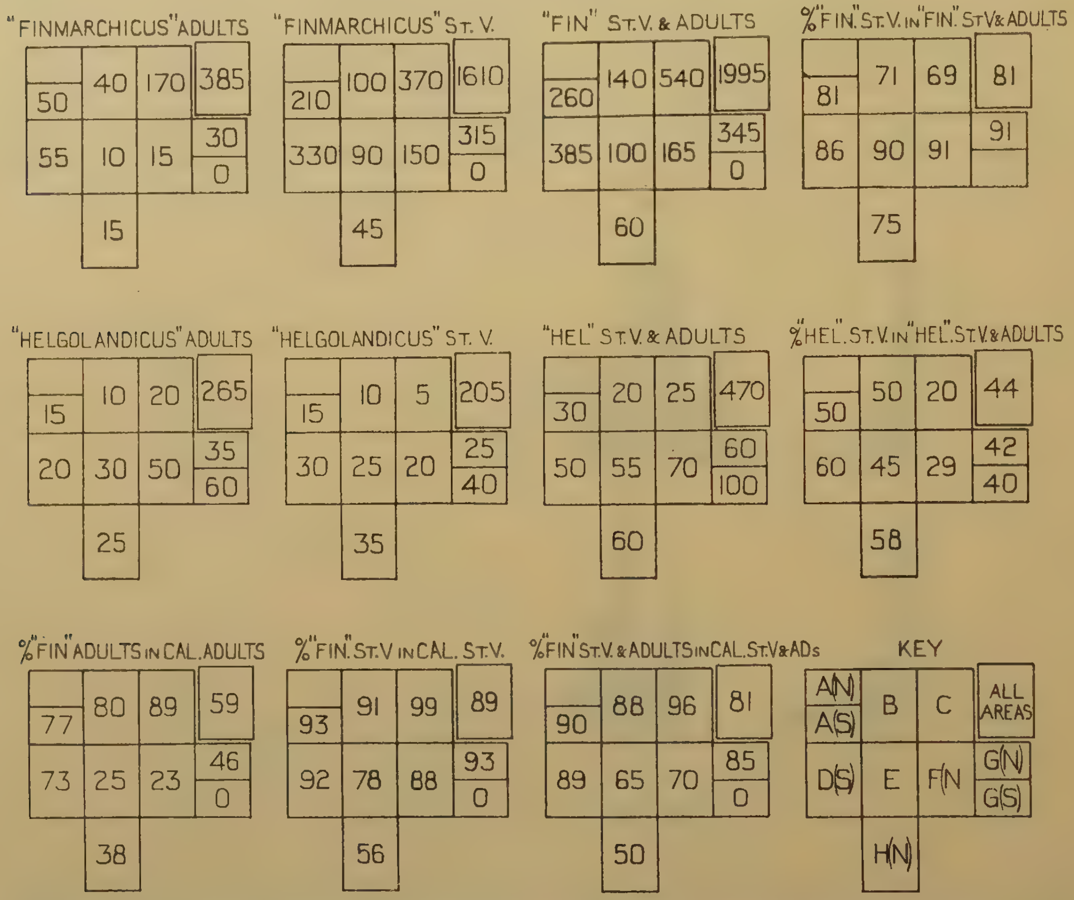
[1] In an investigation of population histories the frequency of sampling is a matter of considerable importance. Normally there was only one record in each month in H(N), G(S), G(N) and F(N), whilst in E, D(S), B and C there were two records in each month. Between April and November there were four records in each month in A(S) and normally two in the remaining months. In A(N) there were two in each month from April to November and none in the other months.

The average numbers per 10 mile unit per month of " finmarchicus " and " helgolandicus " Stage V and adults have been calculated for each of these areas. These data have been grouped in two ways : (1) The monthly averages of all areas have been added together to give corresponding numbers for the combined areas (shown in Text-fig. 5) ; (2) For each area in turn the average numbers per month for the 12 months August, 1938–July, 1939 have been added together to give an estimate, for comparative purposes, of the overall numbers for each area, the results being shown in Text-fig. 6, together with some derived data and a key to the areas.


"FINMARCHICUS" ADULTS
50
40
170
385
55
10
15
30
0
15
"FINMARCHICUS" ST. V.
210
100
370
1610
330
90
150
315
0
45
"FIN" ST.V. & ADULTS
260
140
540
1995
385
100
165
345
0
60
%"FIN." ST.V. IN "FIN." STV & ADULTS
81
71
69
81
86
90
91
91
75
"HELGOLANDICUS" ADULTS
15
10
20
265
20
30
50
35
60
25
"HELGOLANDICUS" ST. V.
15
10
5
205
30
25
20
25
40
35
"HEL" ST.V. & ADULTS
30
20
25
470
50
55
70
60
100
60
%"HEL". ST. V. IN "HEL". ST.V. & ADULTS
50
50
20
44
60
45
29
42
40
58
%"FIN" ADULTS IN CAL. ADULTS
77
80
89
59
73
25
23
46
0
38
%"FIN". ST.V IN CAL. ST.V.
93
91
99
89
92
78
88
93
0
56
%"FIN" ST.V. & ADULTS IN CAL. ST.V & ADs
90
88
96
81
89
65
70
85
0
50
KEY
A(N)
A(S)
B
C
ALL AREAS
D(S)
E
F(N
G(N)
G(S)
H(N)

Text-fig. 6.—Showing in spatial arrangement the sums of the monthly averages of " finmarchicus " and " helgolandicus " Stage V and adults, for each area from August, 1938 to July, 1939 inclusive, together with derived data and, bottom right, a key to the sub-areas.

The graph showing the data for the combined areas (Text-fig. 5) indicates that adult and Stage V " finmarchicus " at 10 m. were most abundant in the spring and summer (April-July), but were quite scanty from August to March. In " helgolandicus," on the other hand, numbers were relatively high from June to October, and the maximum number for the whole period occurred in October, 1938, for Stage V and in August, 1939, for adults. (It may be that the adults continued to increase after August, 1939, for in 1938 the highest number was obtained in October, like Stage V). The spring numbers for " helgolandicus " were much lower, so that it was a distinctly later form than " finmarchicus," partly in its period of first significant increase, but even more in its culmination.

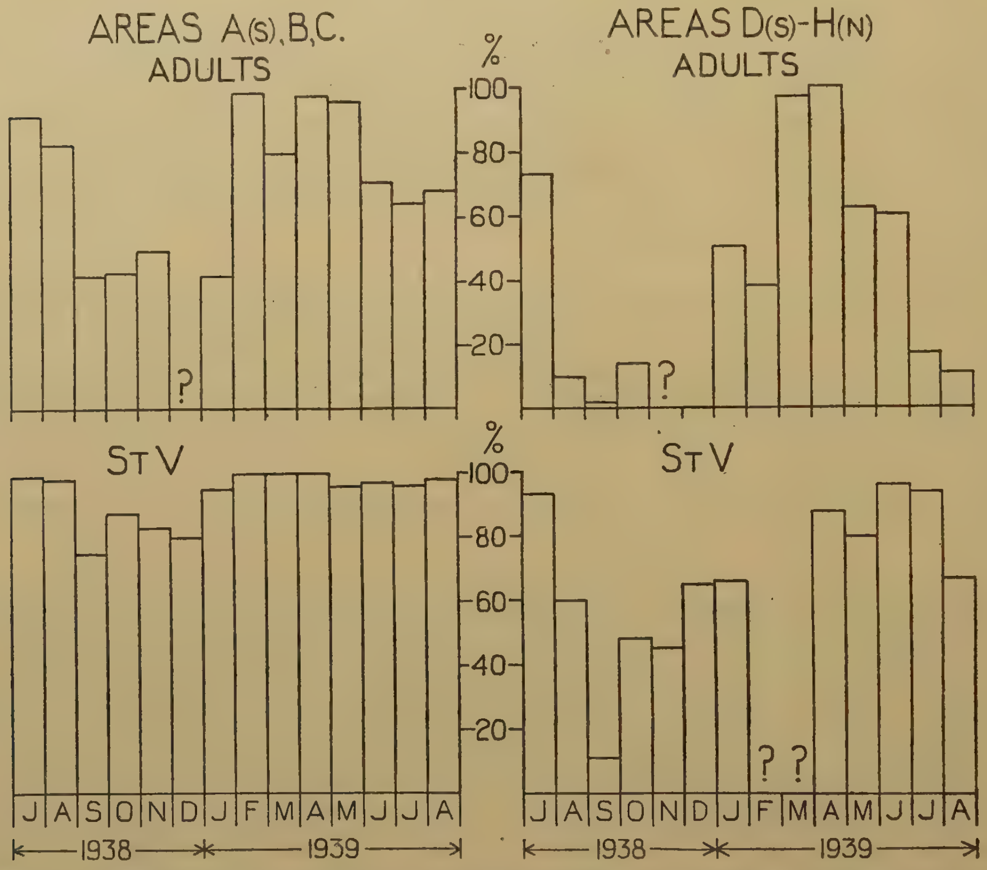
This feature appears again when we follow month by month the percentage of " finmarchicus " in Calanus for each stage. These are given in Text-fig. 7, where the areas have been combined into two groups : A(S), B and C in one, and D(S), F(N), E, G(N) and H(N) in the other. The general predominance of " finmarchicus " at 10 m. in the northern areas is shown, but there was a distinct decrease in its dominance around September–January when, in the adult stage at least, " helgolandicus " was dominant for a time. In general, this seasonal difference is borne out area by area, as well as over the whole region, though there were exceptions.

The best overall estimates available of the relative abundance of the two forms at 10 m. are given in Text-fig. 6. It is remarkable that G(S) produced virtually no " finmarchicus," although the neighbouring G(N) produced very high numbers. In general " finmarchicus " was present in highest numbers in the more coastal areas, whilst the central areas B, E and F(N) were relatively poor. The " finmarchicus " numbers in B, E and H (N) *decreased* from north to south. " Helgolandicus " was much less common and numbers *increased* from north to south.

The percentage of " finmarchicus " in the whole population provides in a single value the relative abundance of the two forms at 10 m. In H(N) (Text-fig. 6), Stage V of the two forms were about equal in numbers, but elsewhere " finmarchicus " was by far the more abundant, except in G(S) where " helgolandicus " was the only form. However, the relations were quite different in the case of adults. In the central and southern areas (E, F(N), G(N) and H(N)) " helgolandicus " was dominant, whilst the dominance of " finmarchicus " was by no means so marked in the remaining areas as in the case of Stage V. In other words, the percentage of " helgolandicus " at 10 m. increased among the adults (see p. 251).

These different relationships are brought out in the remainder of the derived data. Stage V of " finmarchicus " represented some 80% of its combined Stage V and adults, whilst " helgolandicus " Stage V correspondingly represented 44% only. This difference may be more readily appreciable in the form of ratios. The ratio of " finmarchicus " adults to " helgolandicus " adults was 1·5:1, whilst the ratio of " finmarchicus " Stage V to " helgolandicus " Stage V was 7·9:1. Alternatively we see that, whilst there were generally rather more " helgolandicus " adults than Stage V, in " finmarchicus " the Stage V were more than four times as abundant as the adults.

The seasonal extent of these differences between the two forms varied as is seen in Text-fig. 8 (showing the monthly ratio of Stage V to adults in both forms for the whole area). There was no great difference between the forms from January to May, 1939, but from July to October, 1938, and in June and July, 1939, the proportion of " finmarchicus " Stage V was very much greater than that of " helgolandicus." This discrepancy will be discussed later in relation to the life history (p. 252).



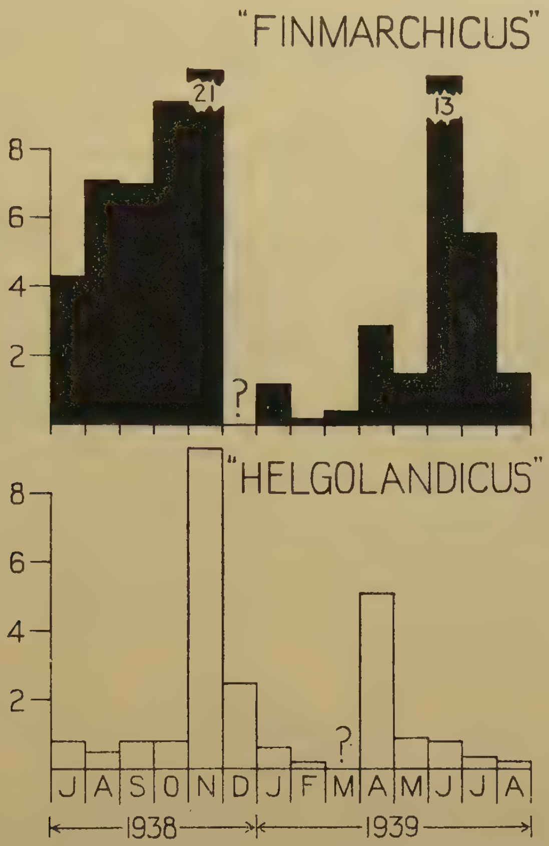
Text-fig. 7.—Histograms showing the mean monthly percentages of " finmarchicus " Stage V and adults in the total Calanus Stage V and adults (" finmarchicus " plus " helgolandicus ") in each of the two area groups (left), A(S), B, C, and (right) D(S), E, F(N), G(N), H(N).

Note on the Distribution of the Two Forms outside the North Sea.

Through the kindness of Mr. P. G. Corbin I have been able to examine the Calanus in plankton samples taken during the cruises of 1938 from the Celtic Sea (South of Ireland), the locations of the stations being given by Corbin (1947). The proportions of the two forms have been determined, where possible, together with some average sizes of the metasome from Stage IV upwards. The results are given in Table I.

Up to 1st June "helgolandicus" was only a little more abundant than "finmarchicus." Afterwards the population was almost entirely "helgolandicus." In all stages "helgolandicus" had the larger average size except in the cases of Stages IV and V from Station 47.

A few samples taken during 1941 in the Clyde Sea area by Professor Hardy and Dr. Lucas have also been examined. Those taken on 29th May, 26th June and 10th July were entirely "finmarchicus," a sample taken on 24th August had a very few "helgolandicus" (less than 5%) and one on 29th September about 30%.



Text-fig. 8.—Histograms showing for all areas combined (above) the numbers of "finmarchicus" Stage V relative to one "finmarchicus" adults in each month from July, 1938, to August, 1939, and (below) similar relative numbers for "helgolandicus."

Both forms are obtained on the eastern end of the Pentland Firth–Iceland recorder line (Lucas, Marshall and Rees, 1942), that is, over the Continental Shelf north-west of Scotland. For example, 30% of the Stage V in June, 1948, were "helgolandicus." Only "finmarchicus" has been identified over the deep water section of this line.

TABLE I.—*The Proportions of "finmarchicus" and "helgolandicus" in the Celtic Sea* (1938). *Average sizes are given in italics.*

Date.	Station,	MALES.		FEMALES.		STAGE V.		STAGE IV.	
		Finmarchicus.	Helgolandicus.	Finmarchicus.	Helgolandicus.	Finmarchicus.	Helgolandicus.	Finmarchicus.	Helgolandicus.
11th April	22	0	2	1	9	7	13	10	10
						2·31	*2·51*	*1·76*	*1·83*
11th April	25	9	11	15	5	8	12	9	11
		2·38	*2·64*	*2·48*	*2·67*	*2·24*	*2·48*	*1·63*	*1·69*
15th April	47	9	11	11	9	11	9	11	9
		2·48	*2·64*	*2·67*	*2·81*	*2·34*	*2·31*	*1·79*	*1·74*
1st June	7	10	10	0	20	10	10	—	—
4th June	25	0	10	0	20	7	3	—	—
24th July	24	0	3	0	20	0	10	0	7
24th July	26	1	6	0	20	0	20	0	10

Two new Atlantic recorder lines have recently been run from Weather Ships sailing from the Clyde, the recordings actually starting from positions north of Ireland. The northern of these two lines extends to Lat. 60°N., Long. 20°W., and the southern to Lat. 54°N., Long. 18°W. Both forms of Calanus are recorded from those portions of both lines which lie over the Continental Shelf (about 20% "helgolandicus" in Stage V in August, 1948). On the northern line "finmarchicus' only has been found over deep water. On the southern line a rich, narrow patch of Calanus was recorded in May, 1948, at the extreme western end, composed almost entirely of "finmarchicus." During the remainder of the year only very few Calanus were recorded beyond the limit of the Continental Shelf, and all examined were "helgolandicus."

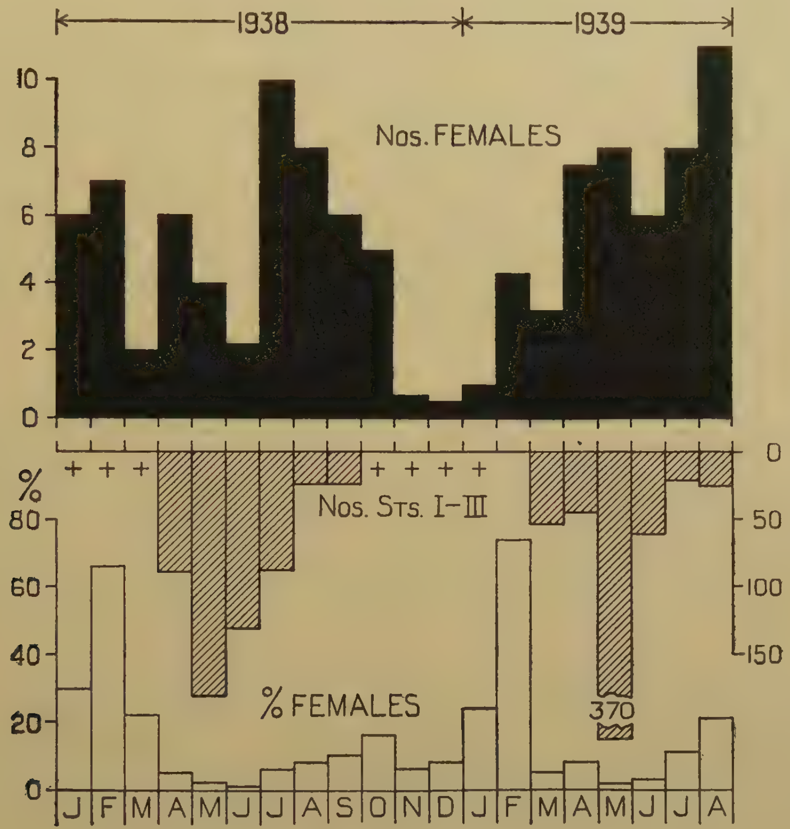
LIFE-HISTORY

Approach to the data.

It has been a common practice (*e.g.* Nicholls, 1933) to consider the life-history of Calanus on the basis of the percentages of the different developmental stages present at any one time. Since the actual numbers obtained by individual net hauls are greatly influenced by the patchiness of plankton distribution, they are subject to large errors of sampling. The consequent fluctuation in the catches render these numbers unsuitable for the tracing of the life history, and the effect of the fluctuations may be reduced by the percentage method. It must not be forgotten, however, that percentages supply only part of the desirable information. Trustworthy information from numbers would include not only this part but also a good deal in addition.

Text-fig. 9 has been prepared in order to illustrate the difference between the information derived from numbers and from percentages. This shows the average numbers of females per month for the northern North Sea areas, in comparison with the monthly percentage of females in the total Calanus catch, and the numbers of young stages (I-III). Without going into detail it is obvious how the information presented by the two methods differs. Over the period March to September the *percentages* of females are largely determined by the varying *numbers* of the much more abundant young stages, and have little relation to the actual *numbers* of females as estimated over a very wide area.

This effect of the abundant form upon the percentage of the less common form is even more strongly marked when eggs and nauplii are also included in the calculations. Such a method places a severe limitation on the data and may well lead to unjustifiable interpretation. For example, Nicholls (1933) stated, on the grounds that the period from peak *percentage* eggs to peak *percentage* females was 4 weeks, that the period of development from egg to adult was 4 weeks. As is shown by Text-fig. 9 (as well as by theoretical consideration), however, a significant peak *percentage* in females is by no means necessarily a guide to the most significant *numbers*. The numbers of females might well continue to increase



Text-fig. 9.—Comparing the monthly average numbers of female Calanus (black histograms), the percentage of females in total Calanus (white histograms), and the average numbers of young stages (hatched histograms, with the scale reading downwards). For explanation see text.

for some time after they reached this peak percentage. Similarly, Nicholls gave the period of maturation of eggs as 3–4 weeks since this period elapsed between the peak percentage of females and the subsequent peak percentage of eggs ; this might be quite misleading.

It is a feature of continuous recording that, while the water column sampled is very narrow, it may be very long in comparison with the usual net hauls, as in the present survey. This results in a considerable " smoothing " of the plankton distribution, essentially reducing the fluctuations to which net hauls are particularly liable, especially those due to patchiness. Also, the main arguments in the subsequent sections of this paper are based on the averages of the estimated numbers for several 10-mile units. This process tends to smooth the fluctuations even further, and thus provides a set of population estimates which can properly be considered in relation to the life history as seen at 10 m. It is not proposed, therefore, in this paper to use percentages when considering the life history of Calanus, but to use only the numbers obtained. This is the more appropriate since at certain times and in certain areas the numbers of Calanus recorded were too low to warrant the percentage method.

General.

Due to its great range and abundance, and its known economic importance, Calanus has received considerable attention. For local waters there is the comprehensive work of Marshall, Nicholls and Orr (1933–35) in Clyde Sea area, that of Gibbons (1933) in the north-west area of the North Sea, of Wimpenny (1936) off Flamborough, and of a number of workers, including Ruud (1929), in Norwegian waters. Russell (1928) worked off Plymouth, and Farran (1927) to the south of Ireland.

The present survey covers a much wider area than any of these, and one in which there is extensive disturbance as a result of water movements. We may first investigate, however, in a general way, how far the life history of Calanus (*i.e.* including both forms) in the North Sea, as shown by recorder collections at 10 m., conforms to the well-established results from other, and more limited areas.

Males were invariably few in number and, as found in other surveys, the ratio of males to females was low. Over the northern half of the North Sea (areas A–G) the proportion of males in the total adults at 10 m. over the 20 months of survey was 15%. The highest percentage of 27% was found in the Forth area (D) and the lowest of 8% in the adjoining area, E. Gibbons (1933 and 1936) found on an average less than 20% in his north-west region.

The important point has been made by Wimpenny (1936) that males occurred in notable numbers only at the spawning periods, of which they appear to be an indication. In the recorder collections males tended to reach peak numbers in January, April, June-July and probably November. Males were at times even more numerous than females (January, 1939, in areas A and B), as Farran (1927) and Nicholls (1933) also found.

A disproportion between the sexes would automatically appear in collections if females live longer than males. Raymont and Gross (1942) found that in culture the average life of a male Calanus was only 1–2 weeks. In large cultures on the other hand, more than half of the females generally remained healthy for 3–9 weeks, this period agreeing with Nicholls' (1933) estimate, from field results, of 6 weeks as the survival period of females. If we allow, then, that females live 3 times as long as males, the overall collections of adults would produce some 25% of males. In *Calanus hyperboreus* a similar disproportion occurs between the sexes and Sømme (1934) has shown that females live perhaps 6 months while the males probably live less than 2 months. Ussing (1938) has explained the disproportion in the adults of Pseudocalanus in this manner and was able to show that the two sexes were practically equal in Stage IV and Stage V.

Marshall, Nicholls and Orr (1934) found that the ovaries of females bearing spermatophores were most frequently in the early state, in which eggs are small and few. This agrees with Sømme's (1934) observations on *Calanus hyperboreus*. It would appear possible, therefore, for a main spawning to occur when males have largely disappeared from the catches. Females bearing spermatophores were rarely seen, so that this useful guide to breeding is not available. (It is possible that the flow of water through the recorder detaches the spermatophores). Attached spermatophores were found from January to October, most of the scanty records occurring in April–May and August. Detached spermatophores have not been recorded.

Text-fig. 10 shows, for each area selected for the study of breeding, the numbers of various stages of Calanus per 10-mile unit at 10 m. at each date on which a record was obtained. For each stage and area there was a succession of peak numbers with a certain logical inter-relationship from stage to stage. For clarification the months which had peaks of Stages I–III, however small, are shown area by area and stage by stage, in a more abstract manner in Text-fig. 11.

The young stages show the most consistent grouping of peak months but it is necessary to distinguish three types of sequence. The localities showing the commonest sequence were B, C, D(S) 1939, E, F(N), G(N). In these the young increased to peak numbers almost uniformly in *August* (1938), *November*, *March* and *May*, with a general increase of numbers in the following *August* (1939). There were practically no peaks in the intervening months and it seems reasonable immediately to postulate for these areas four distinct breeding periods from which the young can be traced through to the later stages in the following manner.

Stage IV is probably the most transitory of the stages dealt with, and the absence or comparative insignificance of some peaks is not surprising.[1] There was a consistent series of peaks for these areas in and around *June*, and some appeared around *August*, in 1938, whilst in *August*, 1939 there was at least a general increase in numbers. Winter peaks, in *November–December*, though slight, appeared consistently. Finally, there were some peaks in *April* (although less consistently than in June, possibly because development was more rapid in early spring).

Peaks are well shown for Stage V in *April* and *June-July*. The grouping from August to January is not very clear, but each area had a peak around

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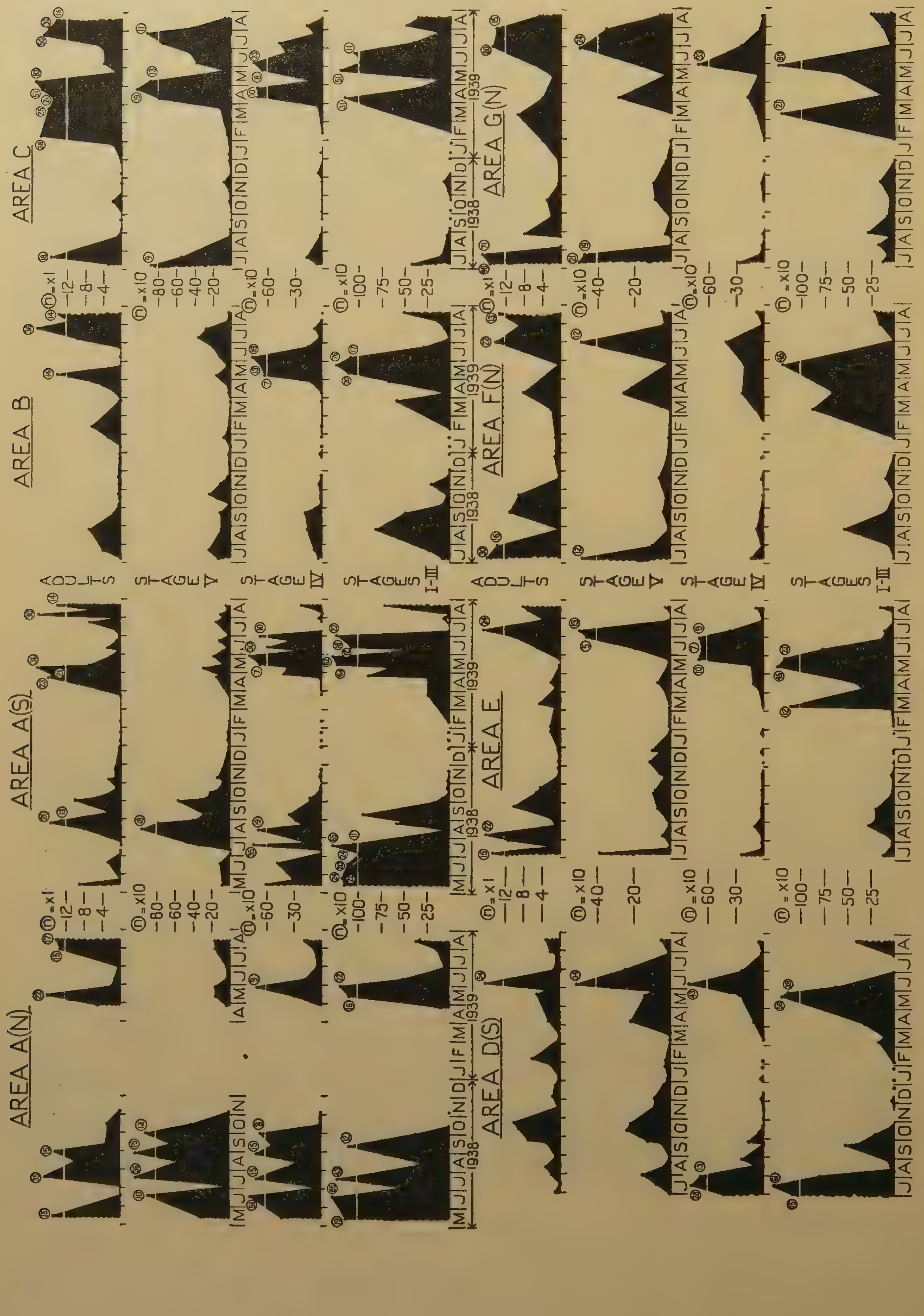
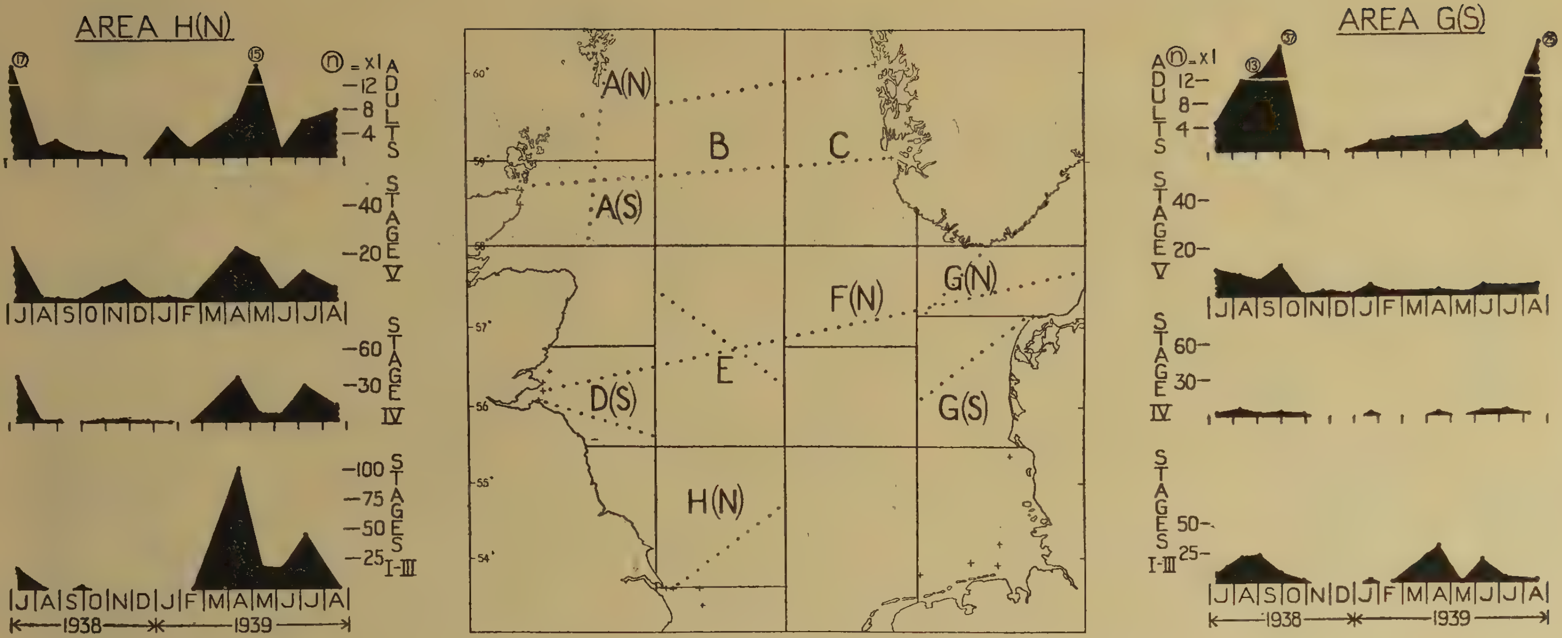
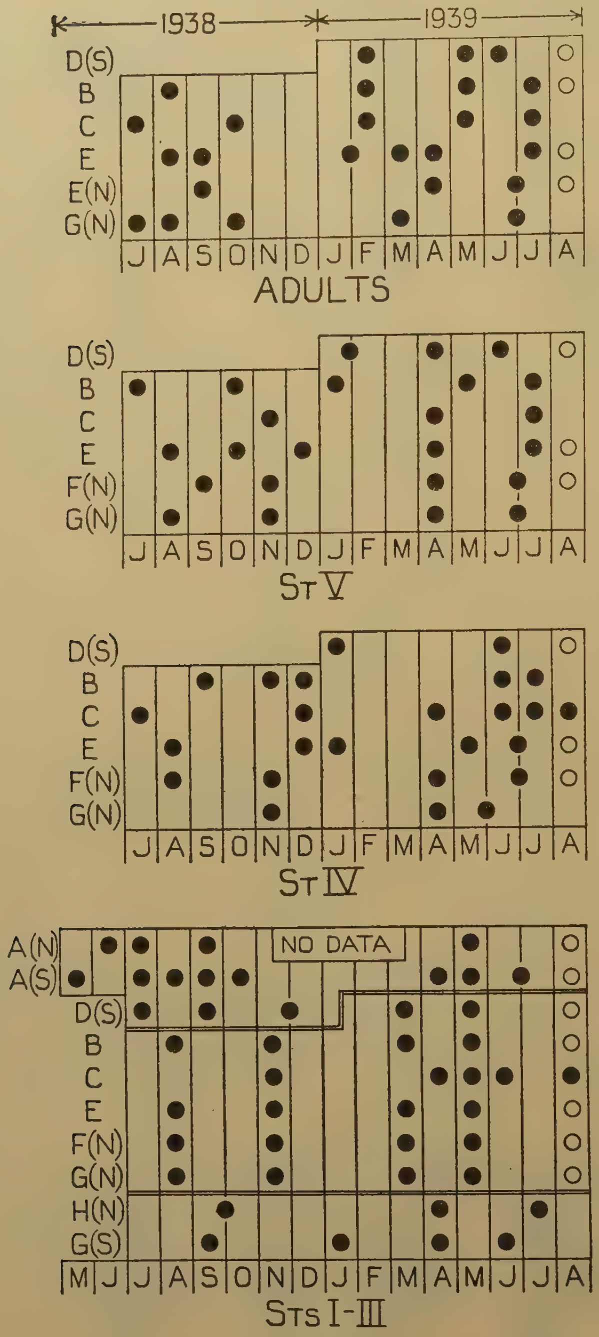
[1] It should be noted that the life of a particular stage of Calanus is relatively short in comparison with the period normally occurring between successive records. For this reason the absence of a peak number for a particular stage may be of no great significance, for the peak number in the sea may have occurred at any time between successive records.


AREA A(N)
AREA A(S)
AREA B
AREA C
AREA D(S)
AREA E
AREA F(N)
AREA G(N)
ADULTS
STAGE V
STAGE IV
STAGES I-III
1938
1939
M J J A S O N D J F M A M J J A



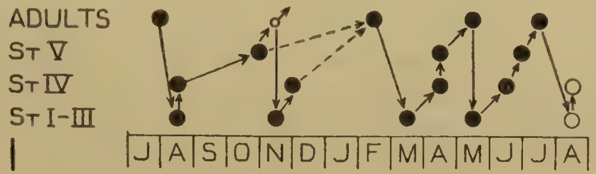
Text-fig. 10.—Showing the average numbers of Calanus per 10-mile unit for the various areas on the dates of each recorder run during part of 1938 and 1939 (a scale of months being shown below the graphs). Four graphs are shown, one above another for the different stages in each area: young stages (I–III) at the bottom, then Stage IV, Stage V and adults at the top. The scale is different for each stage, and has an upper limit above which the numbers are shown within rings. A chart inset shows the boundaries of the areas, the dots representing the centres of the 10-mile units.



Text-fig. 11.—Showing, for each stage, area by area and month by month, the occurrence (●) of peak numbers (however small) of Calanus (abstracted from Text-fig. 10). Open circles (○) for August, 1939, denote that numbers were increasing. Peaks of Stage IV and later stages are abstracted only for those areas having the commonest sequence of peak numbers of Stages I–III. For further explanation, see text p. 239.

November and possibly around August. It will be shown below that the simple relationship of peaks at this time of the year was confused by the mixture of the two forms of Calanus with a marked change in the relative dominance of the two forms (see also Text-fig. 3).

For the adult stage the most definite grouping of peaks centred on *February*, *May* and *July* in 1939. It is much less easy to suggest a significant group in the autumn, mainly because numbers were low and therefore the peaks were less clearly defined. These graphs for adults are mainly determined by the numbers of females, but it will be recalled that males tended to be most numerous in *January*, *April* and *June–July*, and, perhaps, in *November*. The first three of these slightly antedate the major peaks of the females and there can be little doubt that here are the three main parental generations, producing the young of March, May and August. The November males and young lend weight to the evidence for another adult peak in the late autumn.



TEXT-FIG. 12.—The generalized scheme of Calanus breeding in the main part of the North Sea, as derived from Text-fig. 11. For the peak of adults (♂) in November see text p. 238.

Sufficient consistency appears in this series to justify the setting up of a generalized breeding sequence as shown in Text-fig. 12. We may say that, over a wide region, there were four main breeding periods, with peak numbers of young stages in March, May, August and November. Each of these peaks of young stages was followed, more or less clearly, by Stages IV and V to adults, thus providing the parents of the next generation.

In the light of this construction, it is now possible to return to Text-fig. 10 and consider each area separately. Whilst every peak has been allowed for in the abstract (Text-fig. 11), to avoid bias, certain of them appear to be genuinely insignificant, or merely shoulders on a significant peak. Numbering the generations, according to the peaks of the young stages, as 1 (March), 2 (May), 3 (August) and 4 (November), the successions are complete in B, except for the 3rd peak of adults and 1st Stage IV, and in C, except for the 3rd young stages and Stage IV. In D 1939 and E there were no peaks for the 1st Stage IV. In F(N) the February–March adults cannot be distinguished, and in G(N) they apparently merged with the 1st adults. When allowance is given to the fact that there was often a long interval between recordings (particularly in the spring) the agreement between the areas individually and the generalization is perhaps surprisingly good.

There is, therefore, agreement with the results of other workers, particularly regarding the spring and summer breeding. Nicholls (1933), for example, found three plainly marked breeding periods between February and July. The existence of a distinct fourth generation in winter, however, has not been so clearly shown hitherto, although the recorder results are very consistent. Yet there is ample evidence from elsewhere that breeding can occur in late autumn or winter. Gibbons (1936) found eggs in October–November, Wiborg (1940) records spawning in winter in the Oslo Fjord, Runnström (1932) found nauplii in September and October in the fjords at Bergen, and Wimpenny (1936) found eggs on the 5th–15th October cruise in 1934, off the Northumberland coast and off the Humber. Farran (1927), again, found evidence of breeding in November, on at least as large a scale as September.

From our data it is not possible to assess the importance of this fourth generation. If the conditions at 10 m. were representative of conditions at all depths, we might consider the often abundant adults of February--March to have been derived from this fourth generation. We should then have a simple sequence of four generations, with little overlapping, even in the adult stages. However, Gran (1902), Paulsen (1906) and others have shown that the main mass of Calanus spends the winter as Stage V in deep water. Sømme (1934) has studied this deep water winter population closely, and traced its upwards migration in February–March. Taking these results into account it appears possible, if not more probable, that the peaks of adults in February-March were due to such an upwards migration, being mainly derived from the August young. The fourth generation may merely have served to re-inforce to some extent the over-wintering stock of the resultant Stage V from an earlier breeding. In this, it is perhaps significant that the highest numbers of such adults were obtained in area B, in the Skagerrak, G(N), and off Bergen, *i.e.* over the deepest water covered by the survey. Further evidence in support of this view will appear below when it will be seen that the culmination of the fourth generation occurred well before February–March (p. 248).

In another type of sequence, H(N) and G(S), the March and May generations were apparently replaced by a single one in April, (see abstraction of Stages I-III in Text-fig. 11), and the summer generation was moved forward to June-July ; the autumn (September) and winter peaks were somewhat indefinite. Late stages followed through from the peaks of young stages as shown in Text-fig. 10. In the appendix dealing with the Southern North Sea, 1932–39, it will be shown that both single and double spring generations have previously occurred there in different years, with a tendency for April to be the peak spring month ; two other peaks were generally found, in the summer and autumn.

The third type of sequence of peaks of young stages is shown by A(N) 1938, A(S) 1938 and 1939, and D(S) 1938 (Text-figs. 10 and 11). Following the spring peak (May) there was a considerable peak of young stages in July and a secondary peak in September. In A(S) 1938 and D(S) 1938 these July young stages followed through to adults in August, the main difference between the two areas being the greater decrease in numbers through successive stages in D(S), resulting in very few adults in this area. In both areas, too, the September young stages followed through successively to adults around October. In 1939 D(S) followed the more general sequence shown by B, C, etc. whilst in A(S) the young stages followed closely the sequence found in the previous year. In contrast to 1938, however, few Stage V were obtained following the early July peak of young stages. It is difficult to decide how much significance to give to this failure to obtain good numbers of Stage V in spite of the frequent sampling of the area.

The most obvious explanation of the succession in A(S) and D(S) 1938 is that the spring generation took a much shorter time to complete development than in other areas, the adults arising from it breeding at least a month earlier than elsewhere, even than in the adjoining areas B and E.

Such an explanation is hardly possible for A(N). It is clear that in this area the two years were very different, each stage being considerably fewer in 1939 than in 1938, and, furthermore, there was no peak of young stages corresponding to the great peak in July, 1938. Although the sequence of young stages in A(N) 1938 was very similar to that in A(S) there appears to be a marked difference in the later stages. In A(S) there was on the whole a temporal sequence from stage to stage whilst in A(N) 1938 there was a strong tendency for the stages to give peaks together and not in succession. Thus, in 1938, the younger stages up to Stage V gave peaks together in June, all stages in July, and Stages IV, V and adults together in August. The apparent synchronism of the first group in June may, perhaps, be of little significance since there was no sample between 10th May and 18th June. Nearly everywhere else, as in A(N) 1939, most young stages were obtained towards the end of May.[1]

However, there appears no reason to question the synchronism of all peaks in July and Stages IV, V and adults in August, and we may now return to A(S) 1938 with this fact in mind. It will be seen that only younger stages up to IV were synchronous in July, but in August there was another peak of Stage IV at the same time as one of Stage V. This peak of Stage IV has hitherto been disregarded, but if significance is allowed to those in A(N) it can hardly be disallowed here.

Though, in 1939, A(N) and A(S) differed considerably in the incidence of young stages, both areas agree in the low numbers of Stage V throughout, and in the peaks of adults in May and August. The May adults possibly arose from an early spring generation. It is instructive to compare the 2nd generation Stage V peak in other areas with the absence of such definite peaks in the north-west.

The significance of these facts will be discussed later (p. 255). The questions that arise are: (1) What was the source of the July young stages (in A(N) 1938, A(S) 1938–39, D(S) 1938)? (2) What was the source of the stages giving peaks in August (Stages IV–adults in A(N) 1938, Stages IV–V in A(S) 1938, and adults in A(N) and A(S) 1939)? (3) How is the synchronism of peaks in July and August to be explained?

Life-histories of the two forms.

The separate numbers of both forms are shown in Text-fig. 13 from Stage IV to adults, the dates of the peaks of young stages being also indicated. Since Stage IV is the earliest stage that has been separated into the two forms its distribution provides the most direct evidence in the present data of local breeding, although, of course, all other available evidence must be considered.

There were potentially four generations of each form, two in spring (1 and 2), one in summer (3) and one in winter (4). The peaks corresponding to these generations in each form have been numbered accordingly in the figure, the number for the "helgolandicus" generations being enclosed in a square. In addition,

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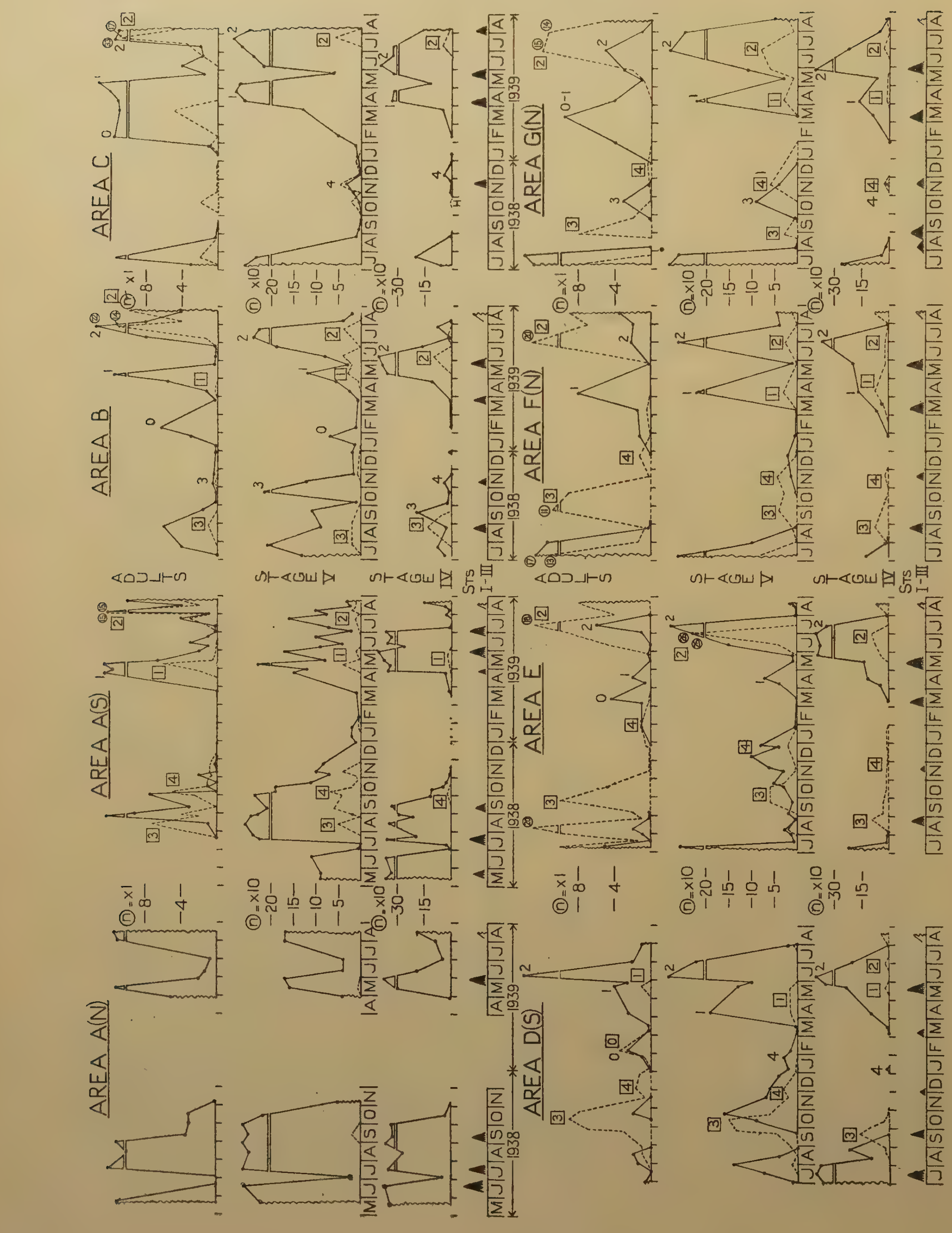
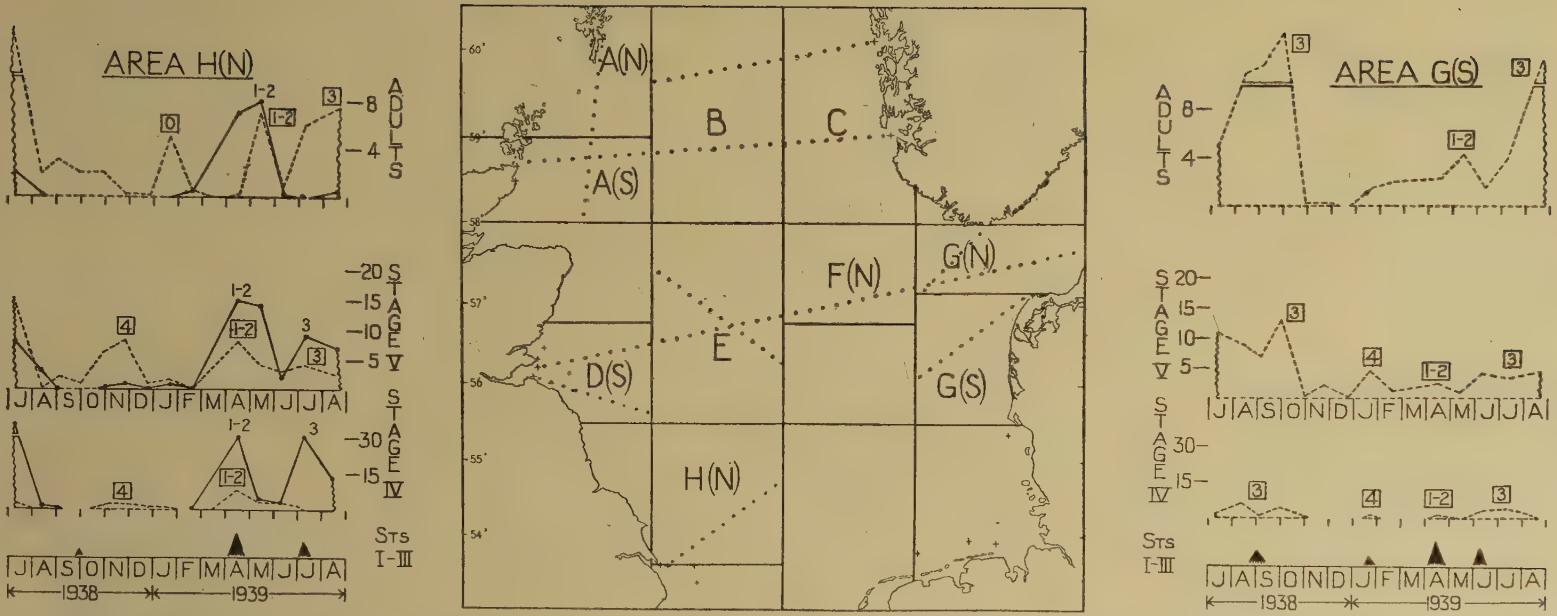
[1] Compare the synchronism of peaks of the 1st generation in F(N) (Text-fig. 10).


AREA A(N)
AREA A(S)
AREA B
AREA C
AREA D(S)
AREA E
AREA F(N)
AREA G(N)
ADULTS
STAGE V
STAGE IV
STS I-III
ⓝ=x1
8
4
ⓝ=x10
20
15
10
5
ⓝ=x10
30
15
M J J A S O N D J F M A M J J A
1938
1939



TEXT-FIG. 13.—Graphs of Calanus Stages IV–adults, arranged as in Text-fig. 10, but distinguishing " finmarchicus " (full line) and " helgolandicus " (broken line) separately. Numbers above the scales (which are variable) are shown within circles only when necessary. Peaks corresponding to generations are numbered 1 to 4 for " finmarchicus," and $\boxed{1}$ to $\boxed{4}$ for " helgolandicus." Peaks of February adults are numbered 0. The incidence of peaks of young stages (I–III) are shown below the graphs for each area by wedges, the tips of which also indicate their relative heights.

the February–March adults have been numbered (0). No attempt has been made to number the " finmarchicus " generations in A(N) and A(S) (see p. 245).

Table II shows how the generations occurred in each area.

TABLE II.

	Finmarchicus.					Helgolandicus.				
	3. 1938	4.	0.	1. 1939	2.	3. 1938	4.	0.	1. 1939	2.
B .	+	+	+	+	+	+	−	−	+	+
C .	−	+	+	+	+	?	−	?	?	+
D(S)	−	?	+	+	+	+	+	+	+	+
E .	−	−	+	+	+	+	+	−	−	+
F(N)	−	−	−	+	+	+	+	−	+	+
G(N)	+	+	+	+	+	+	+	−	+	+
H(N)	+	−	−	+		+	+	+	+	
G(S)	−	−	−	−		+	+		+	

Stage IV Calanus having basipods to the 5th leg with a straight, toothless, inner margin have been distinguished here as " helgolandicus." It may be that basipods with a very few weak teeth also determine a " helgolandicus " form, but that possibility does not enter now, since all the Stage IV examined in area D(S) from September to October, in E from August to January and in F from August to December, 1938, were without teeth. Furthermore, in August, 1939 all the Stage IV examined in D(S), E and F were toothless. Not only are these results for Stage IV consistent, but the increases to peak numbers of " helgolandicus " Stage V and adults in D, E and F following the peak of " helgolandicus " Stage IV in August–September are fully in keeping with the view that there was a third generation of " helgolandicus " in these three localities.

In E and F, too, there was a peak number of " helgolandicus " Stage IV corresponding to the fourth generation. It was a small generation, but consistent results are shown by the peaks of Stage V and adults in December and January, in E, and Stage V and adults in November–December in F. In D(S), though " helgolandicus " Stage IV was not identified in the winter, the fourth generation was shown by peaks of Stage V and adults in December.

Some time after the peak of " helgolandicus " Stage V of the third generation in the central areas there was a peak of " finmarchicus " Stage V. Yet no " finmarchicus " Stage IV was found in these areas which can be associated with these Stage V. The peak numbers of these Stage V were obtained in October in D(S) and in December in E, and F(N), and this difference in time may well be considered too great to allow one to refer the peaks to corresponding breeding in the three areas. Another point of interest is that the peak number was less in E[1] than in D(S) and least in F(N). Again, " finmarchicus " adults were not obtained in the three areas from September to December, except for a small number in D(S) in October. The explanation of these various features will be discussed later. The available evidence at present suggests that while there were third and fourth generations of " helgolandicus " in each of these three areas, there is no reliable evidence of the breeding of " finmarchicus " giving a third generation at the depth of 10 m. in D(S), E and F(N), or a fourth in E and F(N). In D(S) a fourth generation of " finmarchicus " may well have occurred, following the adults of late October. Thus, a very few " finmarchicus " Stage IV were found in January with successive peaks of Stage V and adults.

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[1] It may be noted that the results for E are obtained from an east–west line (Leith–Copenhagen) and north-west–south-east line (Pentland–Hamburg). This accounts for the greater irregularity of the " finmarchicus " Stage V curve.

Unfortunately, the distribution of Stage IV does not help to clarify the third generation in G(N). No Stage IV corresponding to this generation were obtained in 1938. On the record of August 1939 the number of " finmarchicus " Stage IV was less than on the previous record in July, while the number of " helgolandicus " Stage IV increased. The fourth generation (1938) was predominantly " helgolandicus," " finmarchicus " being almost negligible.

Returning now to Table II and Text-fig. 13 we see that the first and second generations of " finmarchicus " occurred in all areas, except G(S), though in H(N) the two spring generations were replaced by one. The third generation of " finmarchicus " occurred in B, probably in G(N), and in C in 1939[1]; whilst it also occurred in H(N), where it was a good deal earlier. It did not occur in the central areas D(S), E and F(N). The fourth generation occurred in B and C and off the Skagerrak, G(N), but " finmarchicus " did not appear to breed after July in the central and southern areas where only two generations were obtained.

The second, third and fourth generations of " helgolandicus " occurred in all the central and southern areas. The first generation was poorly shown. In A(S) all four generations probably occurred and in A(N) " helgolandicus " was almost absent.

The presence of " helgolandicus " in B and C in the latter part of the year was possibly due to invasion by water movements. Lucas and Stubbings (1948) found an invasion of large *Rhizosolenia styliformis* in October, and Marshall (1948) of *Sagitta setosa* in December. These possible migrant " helgolandicus " may have been derived from those of the Skagerrak, G(N), in September.

The adult " helgolandicus " of C in March appear to be quite isolated and cannot be explained, unless they be, rather unexpectedly, an over-wintering stock of migrants.

Discussion.

The four generations.—The best estimates that we can make of the strengths of the different generations depend on the numbers of Stages I–III obtained, since the accumulating effect of mortality is least on these stages and they are least influenced by any seasonal vertical migration. Since the incidence, although not the relative strengths, of the generations in the two forms is so similar, we may conveniently use the combined numbers for this purpose. Had the two forms not been recognized the data could well have been interpreted in terms of one species alone, and this has, in fact, been done above (Text-fig. 10).

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[1] Generation 3 in Table II refers only to 1938. This generation was not traced in area C in this year.

Taking then, those localities which appear to have produced broods in March, May, August and November (B, C, D(S), E, F(N) and G(N)), the mean number per locality (1938–39) was, approximately, 130 for the 1st generation, 590 for the 2nd, 50 for the 3rd and 10 for the 4th. In the 1st generation the very high numbers of young stages in C and G(N) (following the high number of adults of the over-wintering stock) have a considerable effect on the average. Excluding these two, the average for the four remaining localities was 70. Clearly, the May generation was very much larger than the others, the November very small. The May generation at 10 m. was thus of the order of 50 times the November generation and about 10 times the March and August generations.

If it should prove that the two forms are distinct species, then it would not be justifiable to combine the young stages. We may, therefore, consider the strengths of generations as shown by Stage IV, for which we have data for each form. The average values of peak numbers (or numbers at times corresponding to peaks of Stage V when actual peaks of Stage IV were not obtained) for the above six areas are for "finmarchicus": 1st generation 27, 2nd generation 220, 3rd generation 3, 4th generation 1. As far as is known, however, the 3rd generation occurred only in area B with an average number of 19 Stage IV. The relative strengths of the generations is, therefore, very similar to that shown by the young stages.

The relative strengths of the generations of "helgolandicus" as shown by Stage IV in the same 6 areas, is very different: 1st generation 2, 2nd generation 5, 3rd generation 8 and 4th generation 1. Numbers are very much lower and the error of analysis was probably substantial (p. 226), but it appears that the 3rd generation was the strongest.

The May generation of young stages, in which "finmarchicus" was predominant, produced quite high numbers of Stage V "finmarchicus." It is very noticeable, however (Text-fig. 13), that these Stage V were not followed in E, F(N) and G(N) by comparable numbers of "finmarchicus" adults. In fact, the numbers of adults were very low and a good deal less than numbers obtained in May in F(N) and G(N). In C, again, 2½ times more adults were obtained in May than in July, and in B and E the July "finmarchicus" adults scarcely exceeded those obtained in May. In contrast, good numbers were obtained in D(S) following the May generation of young stages, although the large numbers of Stage V and adults were obtained early (beginning of June), whilst elsewhere the high numbers of Stage V were obtained in the beginning of July or later.

In 1938 the decrease in adult numbers from the July young stages was also very marked (Text-fig. 13, in D(S), A(S)).

As a general rule, it would appear that, when high numbers of "finmarchicus" adults were to be expected round July and August, they did not appear in the recorder collections, this feature being most marked in the central areas and less in the northern areas.

In contrast, the available evidence suggests that the 1st generation of young stages tended to produce a proportionately larger number of adult " finmarchicus " and was, therefore, a more successful generation. This is seen, as far as the decrease between Stage V and adults is concerned, in Text-fig. 8.

Returning to the May (2nd) generation, the number of " helgolandicus " adults obtained in E, F(N) and G(N) was higher than the number of " finmarchicus " adults, in spite of the relative scarcity of " helgolandicus " Stage IV. In B and C, too, the relative number of " helgolandicus " adults was very high.

These features are brought out in Table III, where the peak numbers of " finmarchicus " Stages IV to adults are given for each area, the numbers being reduced proportionately to a standard peak of 10 adults, so as to avoid the wide variation in numbers between areas.

TABLE III.—*The Peak Numbers of "finmarchicus" Stages IV, V and Adults corresponding to the 1st and 2nd Generations reduced proportionately to a standard peak of 10 adults.*

	1st Generation.			2nd Generation.		
	Stage IV.	Stage V.	Adults.	Stage IV.	Stage V.	Adults.
B	5	10	10	84	14	10
C	12	24	10	69	34	10
D(S)	25	47	10	89	62	10
E	55	35	10	153	217	10
F(N)	20	27	10	152	468	10
G(N)	42	64	10	668	468	10
Average B–G(N)	26	34	10	202	210	10
Average B–D(S)	14	27	10	81	37	10
Average E–G(N)	39	42	10	324	384	10

This table shows that (1) the decrease between Stage IV and adults was much greater in the 2nd generation than in the 1st, (2) the decrease in both generations was greater in E, F(N) and G(N) than in B, C, and D(S), this being especially marked in the 2nd generation.

From a similar table for " helgolandicus " the proportions in the 2nd generation are 4 Stage IV, and 5 Stage V for 10 adults, and in the 3rd generation 11 Stage IV, 8 Stage V for 10 adults (derived from areas D(S) to G(N) only). These figures show that the adults of the 2nd generation were more successful than the 3rd.

In " finmarchicus " there were usually more Stage V than Stage IV or adults, but in " helgolandicus " there were usually more adults than Stage V (see Text-fig. 6).

An account of the generations in each form was given on p. 249 and we may now briefly summarize the strengths and success of these generations. In " finmarchicus " the March generation was a moderate one and passed relatively successfully to the adult stage. The May generation was very large and passed through successfully to Stage V, but did not give proportionate numbers of adults and, particularly in the central areas, appeared from this point of view to be an unsuccessful generation. The 3rd generation, where it occurred, was only moderate and the 4th slight.

Relative to "finmarchicus" the "helgolandicus" generations were small. The second gave relatively high numbers of adults. The 3rd generation was the strongest but appeared to be rather less successful than the 2nd generation in the adult stage. The 1st and 4th generations were slight.

The differences between "finmarchicus" and "helgolandicus" give rise to three main questions:

(*a*) why so few 2nd generation "finmarchicus" adults were obtained?

(*b*) why "helgolandicus" was so very successful among the 2nd generation adults and only slightly less successful in the 3rd generation?

(*c*) through what means did "finmarchicus" increase in numbers in the central areas and H(N) in October–December?

For the first question, a possible explanation has been considered as based on a seasonal change in vertical distribution. In the present state of our knowledge, such a consideration must be largely speculative, but it appears that such an explanation would not satisfactorily account for the present data. Similarly, neither horizontal dispersion nor predation provides a satisfactory explanation.

The first two questions may, perhaps, be linked through water temperatures. It is generally agreed (*cf.* Sars, 1903) that "finmarchicus" is a northern cold-water form. Raymont and Gross (1942) found the moult to be a critical phase in survival and refer to comparable results by Fuller, Clarke and Bonnet. Surface water temperatures (see p. 265) rose rapidly throughout July to a maximum in mid-August and it is suggested for future investigation that these high temperatures may have proved lethal around the time of moulting of Stage V "finmarchicus." In contrast, it might be expected that the high temperatures would favour the survival and development of the southern warm-water form, "helgolandicus."

As regards the third question, we have already seen on p. 227 a close resemblance between the apparent spread of "finmarchicus" in the September–October and that of the suggested "indicator" species of north-western water, *e.g.* Candacia and Metridia (Rae and Rees, 1947), and Clione (Marshall, 1948). There seems good reason, in view of the data in Text-figs. 3 and 13 to accept the central and southern increase of "finmarchicus" Stage V in the autumn as due to invasion from the north-west. It will be agreed that the evidence for invasion, based on numerical distribution alone, is not so conclusive as in the cases of Candacia and Metridia, and the possible existence of a third "finmarchicus" generation in the central areas, unrevealed in the collections and subject to seasonal vertical migration, has been considered as an alternative explanation. This does not appear, however, to account for the data as satisfactorily as would a theory of horizontal migration. It may, in fact, be considered that the autumnal increase of "finmarchicus," following its summer disappearance, provides the additional evidence from the life-history which was required (p. 227) before

" finmarchicus " could be considered with some certainty as an indicator of north-western water.

The developmental intervals.—Nicholls (1933) has given the most complete estimates to date of various generation periods, although it was indicated above (p. 237) that he perhaps failed to appreciate the limitations of the percentage method, so that some of his arguments may be erroneous.

Sound estimates of the intervals between generations and stages require that the samples should (*a*) give a reliable measure of the numbers present and (*b*) be taken at short intervals of time.[1] The recorder method of collecting with its process of smoothing, satisfies the first condition, but our data rarely satisfy the second condition. This difficulty can be overcome provided there are available sufficient instances of intervals between peak samples, *i.e.* the intervals between two peaks of adults, or between two peaks of young stages, etc. The average of these intervals between peaks will then give a measure of the time between generations, and the greater the number of such intervals averaged the better will be the estimate.

The data of Text-figs. 10 and 13 have been abstracted to provide an estimate of the full generation period. Using only "finmarchicus" data, the mean of 29 intervals is 74 days. If it is admissible also to include intervals for " helgolandicus " the intervals for the generations are :

Generation.	Examples.	Mean period.
1—2	19	69 days
2—3	6	79 days
3—4	8	70 days

The data also supplies an interval of 81 days (six examples) between the peaks of adults in February-March (over-wintering stock) and those of the first generation of adults. Since some of these intervals are based on rather few examples, it can hardly be considered that the differences between the generations are very significant, and it may be said that a generation is completed in 70 to 80 days. (The period between the adults of the fourth generation and the adults of February–March is not covered by a generation interval). Fish (1936) estimated 71–79 days for a complete cycle and possibly 78–81 days between the second and third generation of eggs. Ruud (1929) found that the entire development of Calanus took three months in the Norwegian Sea. Nicholls (1933) gave two and a half months as the probable life of a single Calanus.

Nicholls, from culture experiments, suggested an interval of 28 days between spawning and the appearance of the adult. He found that the period of development of the egg was 1 day, of the nauplii 11 days, of each of copepodid stages I–IV 3 days (minimum), and of Stage V 4 days, thus giving 28 days in all.

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[1] If samples are taken fortnightly and x days separate peak samples, one can say only that peak numbers in the sea could not have been separated by more than $x + 28$ days or less than $x - 28$ days.

The mean interval of development in the present data from the peak numbers of young "finmarchicus" stages of the 1st and 2nd generations to the corresponding peaks of adults was approximately 44 days (11 examples) and from the adult peaks to the young stage peak of the 1st and the 2nd generations was 24 days (10 examples). Whilst it cannot be claimed that these are very satisfactory estimates, it would at least appear that the interval between the young stages and the adults was substantially longer than that between adults and young stages in the early part of the year. However, this result disagrees with the interpretation given by Nicholls (1933). He writes (p. 95): "It appears that the Calanus, having moulted into adults, require from three weeks to one month for maturation of the reproductive organs and for the transference of the spermatophore to the females, and that meanwhile they are subject to a high rate of mortality so that by the time that sexual maturity is reached comparatively few females remain. Thus the egg peak would coincide with the female minimum." According to Nicholls' estimates the period between peak numbers of females and peak numbers of copepodid Stage II should be about 37 days (21 days for maturation of eggs, during which mortality was said to have reduced the numbers of adults, plus 16 days for the moulting of the developmental stages) and that from Stage II to peak numbers of adults about 22 days (allowing one week before mortality sends down the numbers of adults from the peak). These intervals are, proportionately, reversed from those of the present data. Yet it is difficult to believe that Calanus is so inefficient a species that the great majority of adult females die before breeding, and the recorder results are in keeping with the view that the main breeding coincides with the greatest number of females.

It is, moreover, uncertain whether Nicholls' culture experiments support his deductions. There is in fact, field evidence which suggests that under natural conditions, it is unlikely that copepodid Stages I–IV have even approximately equal lengths of life, whatever the minimum may have been on certain occasions in culture.

In the table below are shown the numbers of each copepodid stage obtained by Nicholls (1933) and Marshall, Nicholls and Orr (1934) in the Clyde Sea, and Gibbons (1933) in the North Sea, together with (in heavy type) the values of these for Stages II–VI relative to Stage I as a constant of ten.

TABLE IV.—*The total number of Stages* I–VI *obtained during surveys by other workers and* (*in heavy type*) *the values relative to* 10 *Stage* I.

Copepodid Stage	I.	II.	III.	IV.	V.	VI.
Nicholls, Station I	4138	5549	4071	4939	7728	3222
	10	**13**	**10**	**12**	**19**	**8**
„ „ II	969	1086	1539	4780	29,558	2336
	10	**11**	**16**	**49**	**305**	**24**
„ „ IV	378	564	1305	3145	81,976	1670
	10	**15**	**34**	**83**	**2169**	**44**
Marshall, Nicholls and Orr	3414	6440	8330	8923	32855	13014
	10	**19**	**24**	**26**	**96**	**38**
Gibbons (Northern Area)	1109	3123	6130	6587	6038	2484
	10	**28**	**55**	**59**	**54**	**22**
„ (Southern Area)	2479	3127	3533	5017	6413	2156
	10	**13**	**14**	**20**	**26**	**9**

Marshall, Nicholls and Orr considered that the Clyde Sea was a self-contained area, so that there should have been no influx of water, although we have still to allow for internal differences, possibly including movements. For all that, their data strongly suggest that the numerical increases from Stage I to Stage V (despite cumulative mortality) were due to an increasing length of life per stage, whereby IV may well have lived several times as long as any of the younger stages. Such evidence, incidentally, reflects on Gibbons' conclusions that the increasing numbers of the successive stages (excluding adults), particularly in his northern area, indicated a steady invasion. This may well have occurred, but some appreciable part of this increase may be expected to be due to the increasing length of life of successive stages.

Following a description of the course of events in the north-western areas (p. 245), three questions were raised. Having estimated the interval of development of a generation as 70 to 80 days, we can use this to seek an answer to two of the questions, since in area A(S) samples were sometimes taken sufficiently frequently to determine the estimated maximum period between peaks.

(*a*) What was the source of the July young stages ? Since the peaks of young stages in A(S) 1939 were on 28th May and 2nd July the recorded interval between them was 35 days. If we allow for the dates of the records on either side of the peak records the interval between the actual peak numbers in the sea could not have exceeded 58 days. Even if this period actually approached the maximum, it is still very low in comparison with the estimate of 70–80 days. In 1938 the two peaks occurred at a recorded interval of 56 days, with a maximum of 67 days, which differs less significantly from the estimated mean than in 1939.

If these July young stages resulted from the breeding, in the area, of the adults arising from the May young stages, then the May generation must have developed very rapidly. The alternative explanation is that there was an invasion of young stages in July. This receives support from the fact that in most cases the other species regarded as indicators of north-western water appeared in good numbers or re-appeared, in the north-west, about July-August (Rae and Rees, 1947, Marshall, 1948). Objection may be raised on the grounds that young stages appeared more or less simultaneously in A(N), A(S) and D(S) in 1938, whereas invasion presupposes a succession in time. However, if eggs and nauplii are brought in with the faster moving surface drift and development everywhere is at the same pace, then, over a wide area, there would be a simultaneous increase in copepodid stages.

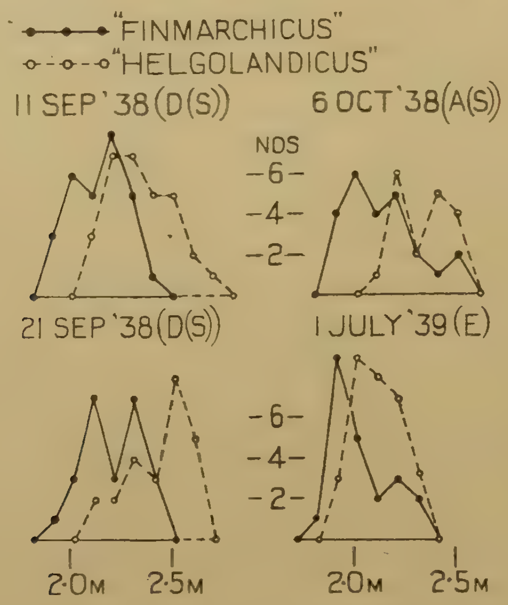
(*b*) The peaks in August ? The test of the developmental interval can be applied in only one of these cases. In A(S) 1938, Stage IV occurred as recorded peaks on 17th July and 14th August, *i.e.* an interval of 28 days. Taking records on either side the maximum interval between peaks was 48 days. This is even shorter than in the case of the young stages just considered.

The peaks of late stages in August, 1938, in both A(N) and A(S) may have been due to a secondary invasion, although the adults of August, 1939, could, conceivably, have arisen from the May or early July young stages. It is, however, a striking feature that, unlike other areas, there was no comparable peak of Stage V in either area. This absence could scarcely have been due to infrequent sampling, and there seems to be no valid reason for not equating these peaks with the peaks of August, 1938.

(*c*) The synchronism of peaks ? This problem applies in particular to area A(N), where samples were taken quite frequently. The synchronism of peaks, therefore, is difficult to understand in relation to local breeding. No such difficulty exists, however, if invasion is assumed. For example, if a large population of Calanus is brought into an area to mix with a low population, then it would show several stages as peaks, though these stages, *within their own population*, would not necessarily be peak numbers.

The proportionate numbers of Stage V obtained by Gibbons in the North Sea are rather low compared with the results of the other workers in the Clyde area (Table IV). This feature resembles the relatively low numbers of Stage V collected by the recorder in the north-west in 1939 (Text-fig. 10). It would appear possible that there was a movement of the late stages around June southwards to D(S), where an unusual production of Stages V and adults occurred at a very early date. Another possibility is that the grazing action of the herring on the Calanus was responsible (*cf.* Savage, 1931, Lucas, 1936). According to Manteufel (1941) the great reduction of plankton in the closed bays of Murman has been definitely established and he found this most effective after Stage IV in Calanus.

Little can be said here regarding the fundamental differences between the two years. It appears, however, that the possible invasion of young stages into the north-west in July was more effective in 1938 than in 1939, while the north-western recession of " finmarchicus " occurred earlier and more strongly in 1939 than in 1938. The development of " helgolandicus," again, was certainly more successful in July and August, 1939, than in 1938. Further, the remaining plankton data reviewed by Rae and Rees (1947), and Marshall (1948) strongly suggests that invasion was either less effective, or at least delayed, in 1939 as compared with 1938. These features may be associated with the fact that 1939 was a distinctly warmer year than 1938 ; the possible influence of temperature on the two forms will be discussed later (p. 265).

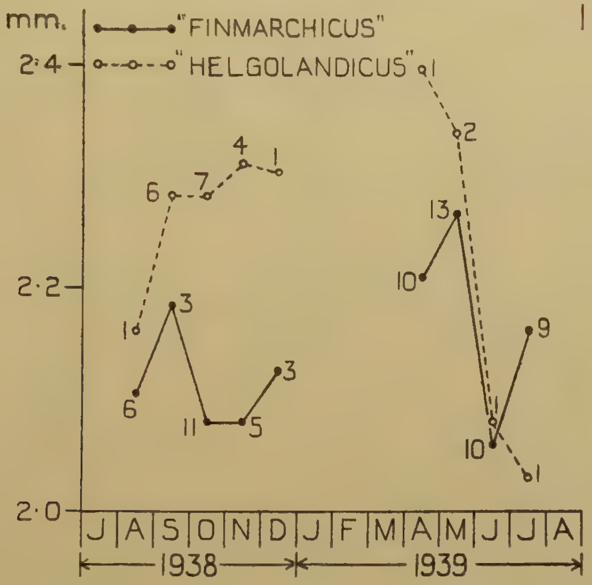


TEXT-FIG. 14.—Graphs showing the size-frequency of " finmarchicus " and " helgolandicus " Stage V from four mixed populations.

SIZE MEASUREMENTS.

As explained on p. 217, the first measurements of Calanus are now known to have included the two forms " finmarchicus " and " helgolandicus " in varying proportions. Most of these results will, therefore, not be reported here. Only those measurements of populations which probably consisted of at least 90% of one form, or which have been determined by measuring the two populations separately, will be dealt with.

While separating the two forms it was very noticeable that in a mixed population, both of Stage V and females, "helgolandicus" was, on an average, larger than "finmarchicus." Owing to the nature of their distributions, it has not often been possible to obtain sufficient numbers of both forms *at the same time* to provide a reliable estimate of their relative sizes. Of fifteen such comparisons, in each "helgolandicus" was the larger, although there was an appreciable overlap in their size frequency, as Text-fig. 14 shows. Because these samples were all obtained at 10 m. depth, there remained the possiblity that they were biassed samples, since the vertical distribution of the two forms need not be similar.



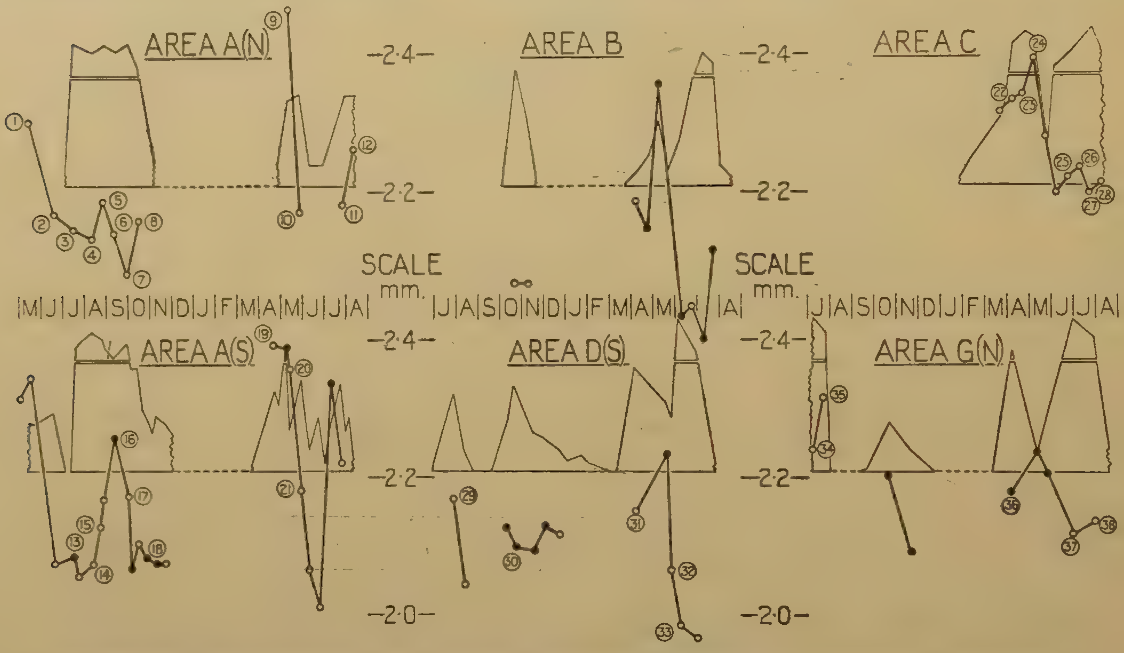
TEXT-FIG. 15.—Graphs showing for each month the mean of all the individual average sizes of "finmarchicus" and "helgolandicus" Stage V recorded. The number of averages used to derive each mean is given against the mean.

However, Dr. J. H. Fraser, of the Scottish Home Department's Laboratory at Aberdeen, who has been separating these two forms from net samples for some time, using Sars' diagnostics, has kindly permitted me to say that he finds "helgolandicus" to be larger at all depths examined (*cf.* p. 221).

For each form all the mean sizes from the various positions, where measurements were possible, have been combined to give a grand mean size each month. These are shown in Text-fig. 15, and against each value is given the number of *mean* sizes on which it is based. Detail should not be read from this figure, since some of the data are based on very small numbers. However, it is clear that from September to December (and perhaps longer) "helgolandicus" was usually much larger than "finmarchicus." The curves from April to July, though based on few measurements for "helgolandicus," show that both forms were then changing in size very similarly.

The mean sizes of " finmarchicus " Stage V obtained on various recorder runs are given in Text-fig. 16 (mean sizes obtained by re-measurement after removal of all " helgolandicus " being indicated by a black circle). To facilitate interpretation of the sizes, the graphs of the numbers of " finmarchicus" Stage V are repeated from Text-fig. 13 where necessary. In each case the base line of numbers has been placed at the same position on the size scale, so that it serves as a convenient guide line, with " large " size-means above and " small " ones below.

Percentage size-frequency curves for populations with not less than 40 measurements are given in Text-fig. 17. The curves have been numbered and the number concerned placed against the plot of average size in Text-fig. 16. Measurements have been grouped in intervals of 0·096 mm.



TEXT-FIG. 16.—Graphs showing the individual average sizes of " finmarchicus " Stage V obtained on various recorder runs in selected areas. Graphs of the relevant numbers of Stage V are repeated from Text-fig. 13 over a base-line, which serves also to distinguish the larger from the smaller sizes. The ringed numbers against some averages refer to the size-frequency curves in Text-fig. 17.

Leaving aside for the moment the north-west areas, A(N) and A(S), we have in 1939[1] a succession of mean sizes for the remaining areas from, or shortly before, the time of the peak in numbers of the 1st generation to shortly after the peak of the 2nd generation. The mean sizes increased up to a maximum in early May (usually on the record following that having the peak number of 1st generation Stage V). Sizes had decreased by the end of May, continued to decrease in June,

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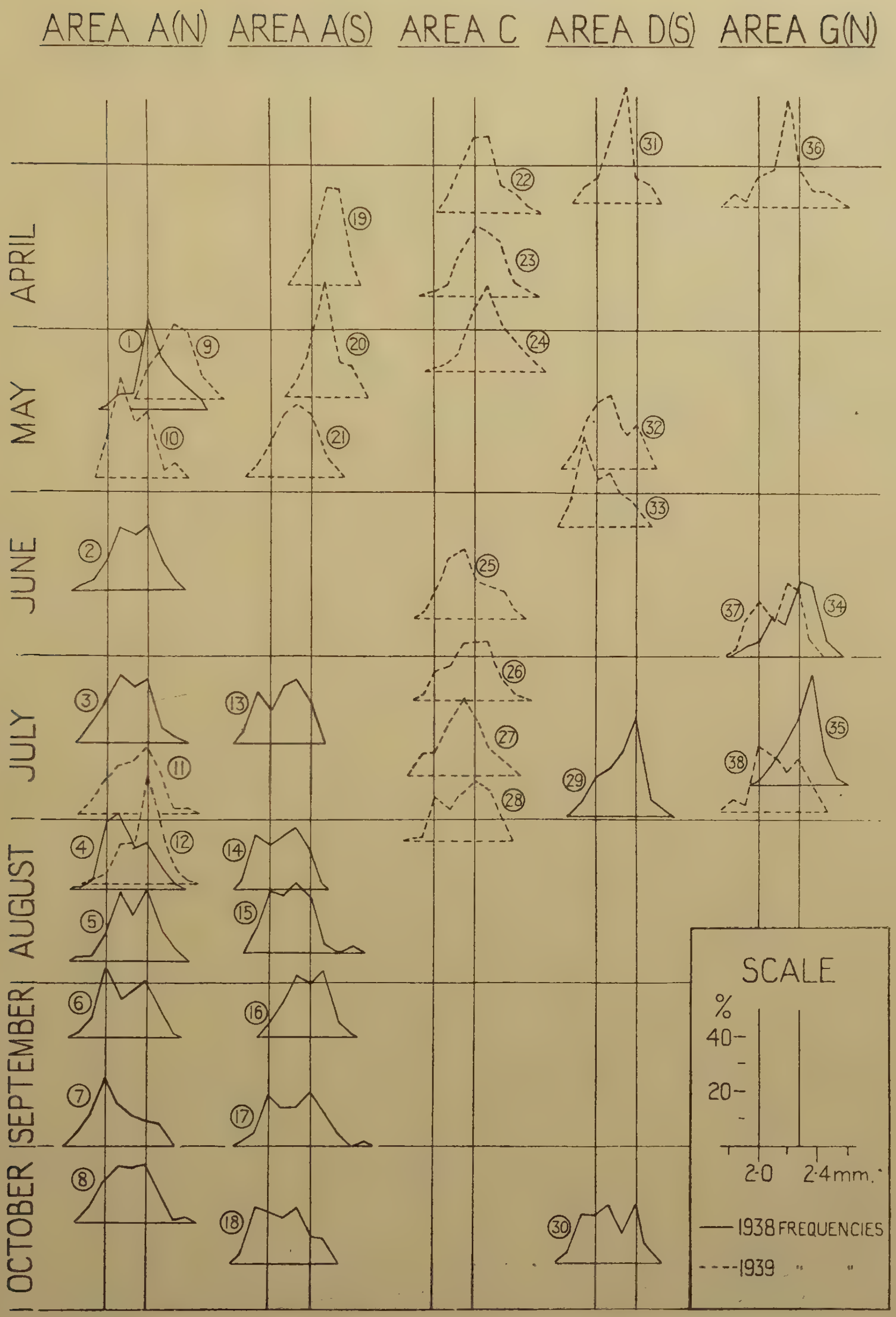
[1] The data for early 1938 are very few, but accord well with the more detailed results for 1939.



Text-fig. 17.—Showing, in date order, selected percentage size-frequency curves of "finmarchicus" Stage V for different areas: those for 1938 in continuous line and those for 1939 in broken line. Each frequency curve is numbered to correspond with the appropriate average sizes, similarly numbered in Text-fig. 16.

and then remained more or less steadily small until after the peak number of 2nd generation Stage V, except in B, where there was a marked increase in size following the peak number. Other fluctuations in size in June–July cannot be regarded as significant.

In the earlier months of 1938 the mean sizes in A(N) and A(S) changed similarly to those of the other areas in 1939, *i.e.* large in May, small in June and remaining more or less steadily small up to and past the peak number of Stage V (July in A(N) and August in A(S)). Thus, as far as mean sizes are concerned, these Stage V " finmarchicus " are comparable with the second generation of Stage V from other areas, though they probably came from a source represented by the young stages of July, and not of May, as in other areas (*cf.* p. 244). The data for 1939 in A(N) and A(S) were generally in accord with those of 1938, up to the end of June. The later changes in both years will be discussed below.

The size-frequencies of the various populations in April and early May were unimodal (Text-fig. 17), but in June they became bimodal with lower size modes.

We can now link up the sizes with the life history over the first and second generations. The early members of the first generation were of medium size. Later members were larger and sizes increased up to the peak in numbers of this Stage V generation. The earlier, smaller members now moulted out of the Stage V population so that the average size continued to increase beyond the time of the peak in numbers. Shortly afterwards (about the end of May) the earliest members of the second generation appeared and the average size fell and continued falling as the second generation replaced the first. There was probably little change in size throughout the second generation.

Following the second generation, Stage V data are, unfortunately, incomplete, except in the north-west areas. It will be remembered (p. 245) that probably only in B and possibly G(N) was there a third " finmarchicus " generation in 1938. Those in D(S) are more likely to be regarded as migrants from the north-west.

In the course of the previous section on life history it became clear that the north-west areas should be distinguished from the rest of the North Sea. The mean sizes in the later months from the north-west cannot, therefore, be considered applicable to the North Sea as a whole. In A(N) a moderate size peak was recorded among those Stage V forms which gave a peak in numbers synchronously with Stage IV and adults in August. The mean size of the members of the peak population in early October (which arose from the September young stages) was very small although sizes increased again at the end of the month. In A(S) the mean size began to increase after the time of the August peak number and continued increasing into early September, when the population of Stage V was at a minimum. Sizes decreased at the peak number of the Stage V which arose from the September young stages, and decreased further on the following record. In both A(N) and A(S), therefore, the majority of the Stage V arising from the September young stages (corresponding in time more with the 3rd generation of other areas than with any other generation) were small.

The October Stage V were small in B (true 3rd generation forms) and in D(S) (source discussed on p. 252), although each mean was rather larger than those of the summer. In G(N), where a true third generation probably occurred, the population forming the peak number was of moderate size and soon became small.

Not many series of measurements over several months are available from elsewhere to compare with the present ones for "finmarchicus." Nor is there any assurance that such measurements refer to only one of the two types, and if so, which one. This applies in at least the data provided by Adler and Jespersen (1920), Marshall (1933), Bogorov (1934) and Wimpenny (1936).

However that may be, there is substantial agreement between the curves for Stage V given by Bogorov (1934) and those in Text-fig. 16. Thus, Bogorov found the size increasing from 11th April to a maximum on 7th May followed by a decrease to a minimum in June. Thereafter the median size changed little up to 3rd September, then dropped rapidly to another minimum on 14th October. Thus, the present results (p. 260) agree with those of Bogorov in that the first generation gives large individuals and the second small ones. The fact that Bogorov found relatively minor variations thereafter is also in agreement with the present data for the greater part of the North Sea. This, in turn, may provide more evidence for believing that the Calanus of the late summer recorded at times in A(N), A(S) and B, which we now know to have been large, were immigrants (p. 255).

Marshall (1933) obtained curves showing only partial agreement from station to station and between stages at the same station. At her stations I and II the median size of Stage V reached a peak in May, dropped to a minimum at the beginning of June, but increased substantially towards the end of June. At both stations females reached the maximum median size a good deal earlier. The curves are interpreted by Marshall as demonstrating that the Calanus produced at the beginning of a breeding period were large, whereas those produced at the end were small. She has accepted the breeding sequence as given by Nicholls (1933), but the error in this interpretation is such that the culmination of one generation may well be mistaken for the beginning of the next, so that the reverse may well have been the case.

Ussing (1938) has explained the size variation of "finmarchicus" in the fjords of East Greenland with marked success by assuming that the size of an individual is determined by the availability of food before moulting. The problem was simplified for Ussing by there being only one period of appreciable phytoplankton and a very small temperature range. In the North Sea the existence of more than one outburst of phytoplankton and the wide temperature range complicates the problem.

There is one important implication in Ussing's assumptions which deserves attention. The size of an individual is the accumulation of increments at all previous moults. With a developmental period of, say 2 months, the environmental factors determining size probably vary quite considerably between the egg and adult. Substantial differences in size may thus easily occur between members of the late stages of the same generation. It is possible that this accounts for the wide range in size of a population, referred to by Marshall (1934). It may also explain why Marshall found the stages, to some extent, to be out of step.

It is considered that the interpretation of the size-changes is one of great complexity, probably involving at least temperature and food supply and the varying impact of these throughout the developmental period. With the data at present at our disposal we cannot usefully attempt to separate out the various factors involved.

GENERAL DISCUSSION.

Certain questions arising out of the Calanus data have been defined above (pp. 252 and 255). While no certain answers to these questions can be given at present, it has often been clear which explanations fit the known facts most closely. In this discussion these explanations are being adopted, and related to a tentative hypothesis of the distribution of Calanus in the North Sea: one which will be liable to modification or even denial as further data accumulate. They imply that:

(1) The name *Calanus finmarchicus* (Gunn.) has usually been applied collectively by ecologists to two quite distinct forms, which appear to correspond with the two species *C. finmarchicus* (Gunn.) and *C. helgolandicus* (Claus) of some systematists. They are, however, so similar in their breeding, in the coincidence of generations and in the manner in which one form replaces the other according to geographical situation, that they may possibly interbreed freely, and, therefore, not be of specific rank. Within the North Sea, they are dominant respectively in the north-western and south-eastern regions.

(2) The large numbers of "finmarchicus" young stages recorded in the north-west in July probably arrived by invasion from outside the North Sea.

(3) The considerable loss between Stage V and adult "finmarchicus" in the central areas in July–August appears to have been due to death at, or about, the moulting stage. This coincided with rapidly rising temperatures.

(4) The subsequent increase in numbers of "finmarchicus" Stage V in both the central and southern areas in October–December is likely to have been due to a transportation by water movements from a source centred in the north-west. Associated were rapidly falling temperatures.

On the basis of these selected explanations it is thought that "finmarchicus" and "helgolandicus" may be members of the same species falling into a cline system (see below), in which the gene complex in the northern forms determines a "finmarchicus" type and in the south-eastern forms a "helgolandicus" type. The major part of the North Sea forms a zone of intergradation, the extent of the zone and the boundaries altering according to season. The balance between the two forms is determined mainly by temperature, warm water favouring the "helgolandicus" type, and the colder water the other.

Excluding the Skagerrak and Norwegian coast, it is probable that normally there is no effective indigenous stock of "finmarchicus" south of about Aberdeen. In August, when the North Sea is at its warmest, "finmarchicus" is eliminated over an extensive area, but it is replaced over the autumn and winter months, in water moving down from the north-west region, which itself receives, in July, large numbers of young stages from outside the area. It is this July invading stock which provides the major part of the stock breeding in the North Sea in the spring of the following year, and annual variations upon the general theme may be expected.

Cline system.—A comprehensive account of clines is given by Huxley (1942). The resemblance between the life histories of both types of Calanus is so close as to suggest the possibility of a free interbreeding (p. 248). The structure of the 5th leg in Stage V and females, however, distinctly separates the two types without a gradation of character. In a typical cline a gradation of characters commonly occurs and it is suggested that the 5th leg of *Stage IV* shows such a gradation; the structure of the basipod varies from the sharp corner bearing several teeth to a smooth margin without teeth. In this work the separation between the two types has been made on the presence or absence of teeth but it is realised that, at present, the only justification for so delimitating the two types is that of practical necessity. It is probable that other diagnostic characters also grade. The shape of the forehead as given by Sars (1903) is quite a distinctive feature, and were there no gradation between the two types it is felt that greater weight would previously have been given to this distinction. Farran (1905) refers to specimens from the west coast of Ireland as being intermediate between *C. finmarchicus* and *C. helgolandicus* after Sars in the outline of the head and proportion of the furcae.

For the purpose of the present work the only diagnostic feature for females which has received attention from among those given by Sars is the shape of the forehead. It was said above that " finmarchicus " and " helgolandicus " (as fixed by the basipods) can be separated from a net collection solely by the shape of the forehead. This has been done for net collections from the North Sea and Clyde Sea area. Females which have, in the words of Sars, a " frontal margin broadly rounded and forming together with the dorsal one, a perfectly even curve " are " finmarchicus " type. Those not having a perfectly even curve are " helgolandicus." Amongst the " helgolandicus," however, the curve varies from being very nearly round to as distinct a narrow curve as given in the drawing of Sars. There is, in fact, a gradation in this character, and, although it has been found only in the " helgolandicus " type, it may not necessarily always be so. The genes responsible for basipod, forehead, furcae, width of body, etc., may, at least in part, recombine independently. There is, too, no difficulty in having one character which is clear cut, like the basipod shape, and others which grade. We may well have here a gradual differentiation of characters.

Despite the graded nature of several characters, the clear cut difference between the basipods is such that the two forms may still deserve subspecific rank, and not be regarded merely as varieties. It follows, too, that the cline would be a dimorph-ratio cline (Huxley, 1942, p. 222).

The zone of intergradation.—The distributions in Text-fig. 3 can, therefore, be thought of as illustrating fluctuations in a cline system, with " finmarchicus " as the northern form and " helgolandicus " as the south-eastern form. The zone of intergradation would be that in which both forms occur.

The ecological pressure of " finmarchicus " was greatest from May to July, and least in late August and September. In subsequent months invasion from the north extended the range of " finmarchicus," and within this extension lie the qualities of " finmarchicus " Stage V as a north-west indicator form.

The most noticeable feature is the contraction of the " finmarchicus " zone northwards in August and September. It is possible that this resulted from rising water temperatures but, unfortunately, there is adequate information only of surface temperatures. In the 'Bulletin Hydrographique' for 1938 and 1939, the thermograms from the Stavanger–Newcastle route for lat. 55° 55′–56° 10′ N. long. 0° provide data for sub-areas D(S) and E. Route 32 crosses H(N), 35 crosses F(N), and 33 crosses G(N). The changes in temperature distribution are such that it *looks as if* a surface temperature exceeding 15°C. may cause the virtual elimination of " finmarchicus," at least at 10 m. depth. Thus, in D and E the surface temperature increased from 14·5°C. at the beginning of August, 1938, to over 17°C. in the middle of the month.

In August the stratification of temperature is considerable and, if it is true that there was a heavy mortality due to the temperature conditions, the effective temperature must have been lower than 15°C. since our material came from 10 m. depth.

This mortality appeared to be heaviest when Stage V should have been moulting to adult. In H(N), following an early summer breeding, fair numbers of Stage IV were obtained in July and a few " finmarchicus " Stage V in August. This may suggest that survival under warm temperature conditions is better in moults of the earlier stages than in the moult between Stage V and adult.

The source of the " finmarchicus " form in the North Sea.—It has been pointed out above that the high numbers of north-western young stages in early July (area A) probably appeared too soon after the peak in May to have arisen from local breeding. It is even more important that these young stages appeared in the north-west at approximately the same time as the north-western indicator species (*cf.* Rae and Rees, 1947 and Marshall, 1948). It is especially for this reason that these young stages are to be considered as invasion forms.

Their source is not precisely known but it is probable that they arose from a heavy spawning about a month after the main spawning in the North Sea. From the records of the Faroe-Shetland Channel (Lucas, Marshall and Rees, 1942) it is known that the main spawning here took place at the same time as in the North Sea, and it is therefore unlikely that the young stages came from this source, though they may have come from somewhere north of the sampled region.

However, the spreading southwards of " finmarchicus " through September to January, together with the north-western indicator species, can be regarded as a definite invasion. Furthermore, if it is true that " finmarchicus " was virtually eliminated from the North Sea south of about Aberdeen in August, then the " finmarchicus " in the North Sea in the early part of 1939 was a new stock which originated in the invasion forms from the north-west. During the spring this stock found a suitable breeding environment in the North Sea and bred extensively, only to be eliminated again when summer temperatures became too high.

Generally speaking the " helgolandicus " population was at a low level. It would appear that its North Sea stock is almost self-contained. From the economic point of view the " finmarchicus " stock is of much greater importance.

These considerations suggest that the extent of " finmarchicus " in the North Sea depends on two factors :

(*a*) the extent of the invasion in the latter half of the previous year, and

(*b*) the suitability of the environmental conditions for breeding in the spring of the year.

Since the first factor can be investigated, the forecasting of the " finmarchicus " stock in the North Sea may become possible if the second factor is not very variable.

The Skagerrak.—The conditions in the Skagerrak require a modification of the hypothesis. The surface temperatures in August were much above 15°C., and mortality may well have occurred, but the re-appearance of " finmarchicus " late stages in October might be the result of local breeding, or of invasion. Low temperatures are available in the relatively deep water of the Skagerrak and it is possible that breeding of the 3rd generation took place in these cold waters, late stages from this breeding rising towards the surface in October. Certainly, in consequence of the deep water in the Skagerrak, the effect of seasonal vertical migration was pronounced at 10 m. later in the season.

Whether or not the " finmarchicus " stock in the Skagerrak is an isolated community cannot be determined from our data. There is available in that region, however, such comparatively deep water that a " finmarchicus " community could probably maintain itself even without recruitment through the deep currents.

General.—If it should prove that " finmarchicus " and " helgolandicus " are of specific rank, the cline concept would have to be abandoned, but the remainder of this hypothesis might still be substantially supported. The evidence at present available is that the two forms differ sufficiently in their habits and seasonal success to make their distinction necessary in most ecological work.

SUMMARY (1938–39).

1. Material obtained during the continuous plankton recorder survey of the North Sea in 1938–39 has been analysed to show the detailed distribution, life-history and size of Calanus at 10 metres depth.

2. Calanus was much more common in the north and was relatively rare south of lat. 55° 30′ N. In the south numbers decreased from west to east. Numbers were at their highest in May (p. 222).

3. The proportion of Calanus to other Copepoda decreased from north to south. Only off Bergen was Calanus the predominant copepod throughout the year, but it was also predominant in winter and/or spring in other localities, even so far south as the Humber (p. 225).

4. The life history of Calanus during the period July, 1938–August, 1939 suggested that generally there were four generations over a year. At 10 m. the 1st generation gave moderate numbers of young stages in March, the 2nd very large numbers in May, the 3rd moderate numbers in August, and the 4th very small numbers in November. Each of these broods of young stages are traceable through to adults (p. 239). Off the Humber and Danish coasts, in 1938–39, there was only one spring generation, in April, and the summer generation occurred in June-July.

5. The mean span of development of a generation was some 70–80 days, between young stages and adults about 44 days, and between adults and young stages about 24 days. In the light of these intervals those presented by Nicholls (1933) have been reviewed (p. 253).

6. By the structure of the 5th legs of Stages IV, V and adults, two forms, " finmarchicus " and " helgolandicus," are easily recognisable. It is not known whether these forms are of specific or sub-specific rank, although they appear closely to resemble the species *C. finmarchicus* (Gunn.) and *C. helgolandicus* (Claus) which have rarely been distinguished by ecologists (p. 219).

7. " Finmarchicus " was a northern form and much the commoner. " Helgolandicus " was relatively uncommon and, in distribution, resembled the central North Sea copepods *Labidocera* and *Isias* but with a much wider range to the north. " Finmarchicus " reached its highest numbers earlier in the year than " helgolandicus " (p. 226).

8. In the spring and summer " finmarchicus " was the dominant form in all areas, except the south-east. In August there was a marked north-westerly contraction of the " finmarchicus " zone, and by September " finmarchicus " was quite rare and less common than " helgolandicus," except in the north-west. Thereafter, the distribution of " finmarchicus " Stage V, extending southwards, resembling that of a typical north-western indicator species (p. 227).

9. The 1st and 2nd generations in " finmarchicus " were pronounced, particularly the 2nd. The 3rd and 4th occurred only in the northern North Sea and the Skagerrak. In " helgolandicus " the 1st generation was very small and often absent. The 2nd and 3rd generations were the main ones and the 4th slight (p. 251).

10. As a rule, when large numbers of " finmarchicus " adults might have been expected in July–August, they were not obtained. In contrast, relatively large numbers of " helgolandicus " adults were obtained (p. 250).

11. The north-west did not conform to the main part of the North Sea in the sequence and timing of generations. There is some reason to believe that a major invasion of young stages occurred in July followed by a secondary invasion of later stages in August (p. 255).

12. In the North Sea, when both forms were present together, the average size of " helgolandicus " was greater than that of " finmarchicus," particularly in the latter part of the year (p. 257).

13. "Finmarchicus" Stage V of the 1st generation increased in size to the maximum for the year in early May. The 2nd generation was small and changed little in size. The main bulk of the 3rd generation was small, the appearance of larger sizes in the north-west, after the May maximum, probably being due to invasion from the north (p. 260).

14. A tentative hypothesis of the distribution of the two forms of Calanus in the North Sea is advanced, in which it is suggested that the apparent replacement of "finmarchicus" by "helgolandicus" in the central and southern waters during the late summer may be due to the local high temperatures having a harmful effect on the former and favouring the latter. The subsequent re-stocking of these waters with "finmarchicus" must be dependent on the strength of invasions from the north-west during the previous autumn. It is suggested that the two forms may be related in a cline system.

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APPENDIX

DISTRIBUTION OF CALANUS IN THE SOUTHERN NORTH SEA, 1932–1939.

by

C. B. REES, M.Sc.

This appendix is supplementary, not only to the foregoing report but also to that on the Copepoda of the southern North Sea, 1932–37 (Rae and Fraser, 1941).[1] The introductory sections of the latter report are relevant but need not be repeated here, except to emphasize that the methods used were less precise than in 1938–39, and only permitted a general division of Calanus into " large " and " small." The former were chiefly Stage V and adults and the latter stages I–IV. Only occasionally was a larger Stage IV included in the " large " category. It has not been possible in the older material to determine the proportions of " finmarchicus " and " helgolandicus."

Owing to the low numbers of Calanus recorded the expense of producing charts of distribution as for other copepods is unwarranted, and the information has been concentrated in the form of histograms showing average numbers per month. The data have been grouped into the areas H, J and L, in the same manner as for 1938–39 (p. 217), but the new routes begun in January, 1938 have been neglected to preserve continuity. Only records between Hull and Copenhagen (C), Bremen (B), and Rotterdam (R), and between London and Esbjerg (E) are considered here. Comparison of the relevant parts of Text-figs. 2 and 18 show that no essential data are lost by this process.

Information for area H has been derived from the western ends of the C, B and R lines. For J the appropriate sections of the C and B lines are included and, after 1936, the middle section of E. For area L the southern parts of the R and E lines have been used.

Text-fig. 2 shows that the numbers of Calanus in 1938–39 to the south and south-east of about lat. 55° 30′ N. were very low, the largest numbers being obtained in the spring and summer months of 1939. Text-fig. 18 now shows that it was typical for the highest numbers in areas H and J to occur in spring and summer, when small stages were common ; on the other hand, the larger Calanus were sometimes as abundant in the autumn and winter as at other times. In area L, however, the higher numbers were regularly found in late autumn and winter, except in 1937. These were almost all larger Calanus and it is clear that they occurred at times when the general copepod population was concentrated against the southern continental coast. In a general way, therefore, success or failure of this section of the Calanus population is correlated with that of the Total Copepoda (' Bulletin ' No. 4), and it is likely that its distribution is probably

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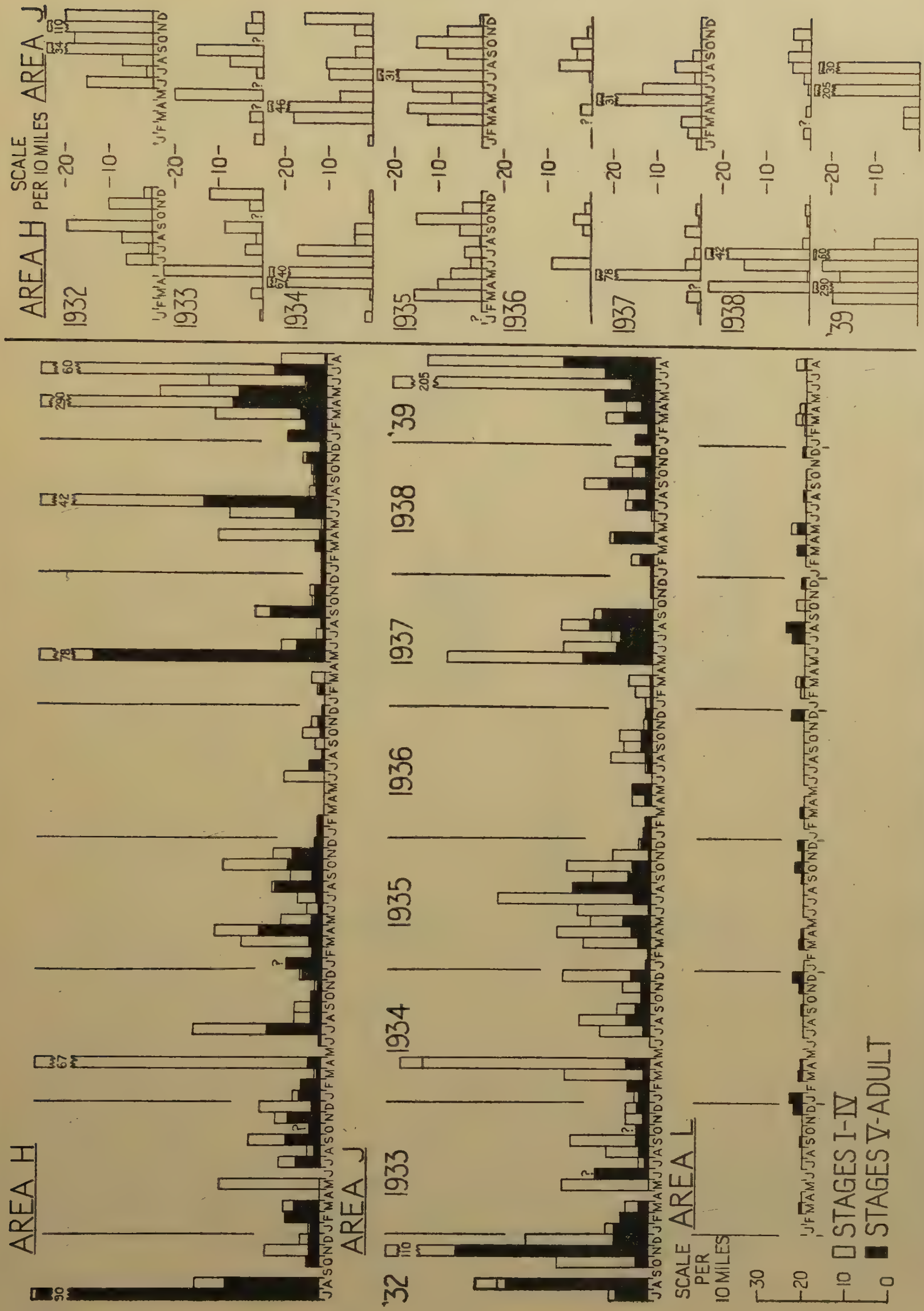
[1] References to literature and text-figures (except 18–20) refer to text and text-figures in the foregoing paper.



Text-fig. 18.—Histograms showing on the left the average numbers of Calanus Stages V + adult (black) and Stages I–IV (white) per month per 10-mile unit in areas H, J and L from 1932 to 1939. On the right the histograms for Stages I–IV have been repeated for annual comparison.

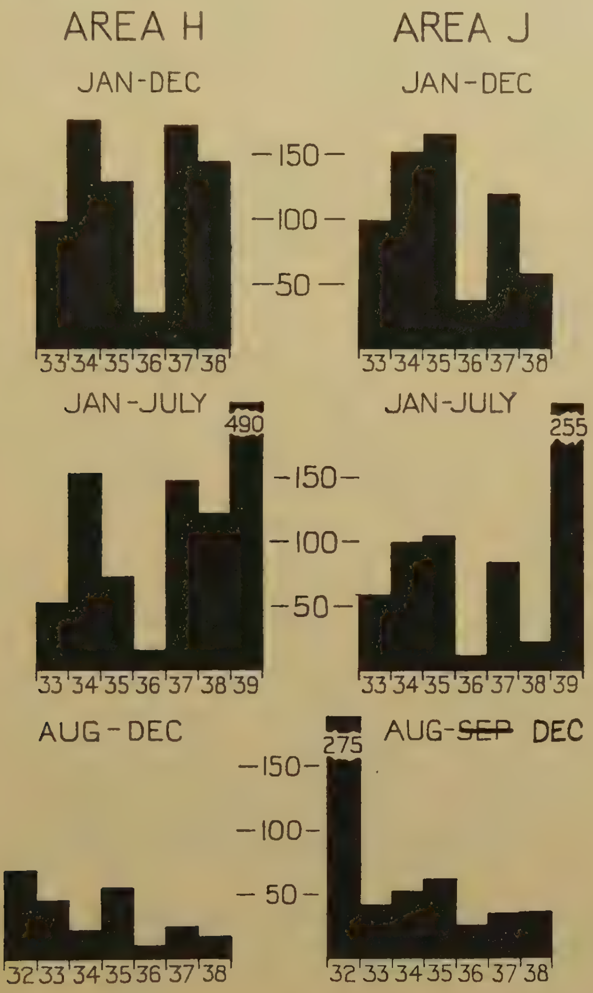
caused in some way by the water movements. Practically no young are there, and it is unlikely that there is any breeding. In other words, L is not in any sense a Calanus area, probably an important point in relation to the feeding of the southern herring after spawning. It is also unlikely to be the " home " of " helgolandicus," as Sars may be considered to have inferred. As far as the North Sea is concerned, the home of " helgolandicus " must be further north (Text-fig. 4).

Some measure of the relative success of Calanus in different years can be obtained by summing the monthly averages for each ; these sums are plotted in Text-fig. 19 for H and J, the numbers for L being too low to deserve illustration. These values are necessarily imperfect, partly owing to the absence of data in certain months (when interpolation has been necessary), and partly owing to a tendency (shown in Plates LXXIV-LXXVII and LXXXV for 1938–39) for the chief patches of Calanus in these waters to be very small. However, accepting such estimates as the only ones available, it appears that 1936 was quite the poorest year of the period in both H and J (and also L). The years 1934 and 1937 were the richest in H, and 1934 and 1935 in J. (The richest year in L was undoubtedly 1937.)

The detailed results for 1938–39 showed that area H was, largely, occupied by " finmarchicus " from January to July. To the east and probably to the south, " helgolandicus " was predominant throughout the year. It was also found that " finmarchicus " reached its highest numbers in the first part of the year and " helgolandicus " later. In recognition of these features the sum of the monthly averages for the period January–July and for August–December have also been plotted in Text-fig. 19.

We can now compare 1932 and 1939 for these periods with the other years. Numbers obtained in the first part of 1939 were exceptionally high in both areas and the latter part of 1932 gave the highest number of all years. Text-fig. 19 shows that the numbers obtained between January and July were higher in H than in J, whilst J had rather higher numbers from August to December. Yet the sum of the yearly totals from 1932–39 gives 1290 for area H and 1160 for area J, so that, overall, the two areas were quite similar. In H, however, 81% of the total was obtained in the period January–July, but in J only 54%. Overall, Calanus was more than twice as abundant in J as in H in August–December.

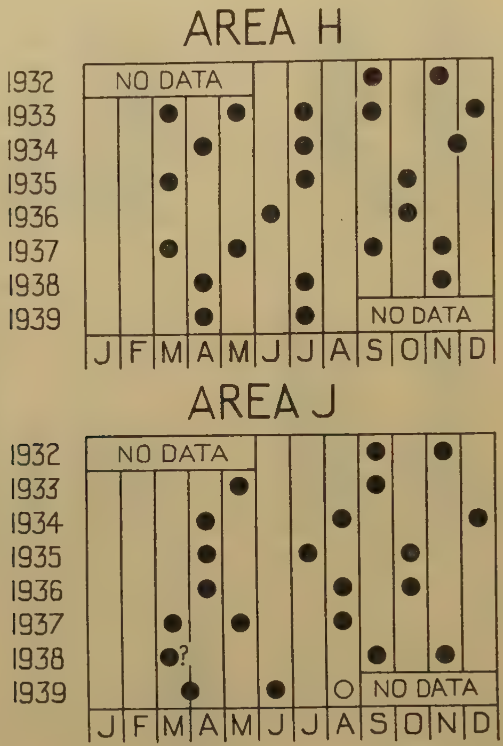
Apart from the high numbers in 1932 and 1939 the most noticeable feature is the very low number of Calanus in 1936, particularly in the period January–July. These low numbers may be associated with those of several other species (see for examples, Rae and Fraser, 1941, Lucas, 1940, and Henderson and Marshall, 1944), and may possibly be correlated with the very low salinities of that year (*cf.* Lucas and Rae, 1947). In particular, Lucas refers to the trend of *Rhizosolenia styliformis* as increasing up to 1935, decreasing in 1936 and recovering in 1937. This last feature may be important, since it now appears that the species *R. styliformis* may be subdivided, at least in size, into two stocks, of which the smaller corresponds roughly in distribution with " finmarchicus," whilst the larger generally occupies the area found here to be more typical of " helgolandicus " (Lucas and Stubbings, 1948). There is not, however, any obvious relationship between the overall developments of Calanus and Rhizosolenia in the southern North Sea during 1932–39, but rather the reverse.



Text-fig. 19.—Histograms showing the sums of the monthly averages of Calanus (Stage I—adults), per 10-mile recorder unit, for January–December, January–July and August–December, 1932–1939, in areas H and J.

The available data from the southern North Sea are by no means as suitable for the study of the life-history as are those for the more densely populated northern areas. Nor only is there less information concerning the different stages of Calanus, but its very patchy distribution in the southern North Sea is a disadvantage in this respect. However, over a long term of years, it is possible to obtain a useful estimate of the chief periods.

The most useful indications of the breeding periods should be provided by the numbers of small Calanus, *i.e.* principally Stages I–IV. If these (illustrated in Text-fig. 18) are abstracted in a similar manner to that used before (Text-fig. 11 and p. 239), the sequence of apparent breeding periods for areas H and J is that illustrated in Text-fig. 20. (There are insufficient young stages in area L for any deductions to be drawn and it is most unlikely that significant breeding occurs there). It appears that in area H the young stages peak most consistently in July and it is, therefore, likely that a generation is initiated in June or July. There then remain two obvious groups of peaks which centre around April and October.



Text-fig. 20.—An abstraction from Fig. 18, indicating the months (●) in which peak numbers of Stages I–IV occurred during 1932–39. The open circle (○) denotes that the numbers were increasing.

The grouping of peaks round April is rather diffuse, and in 1933 (and probably 1937) there were two distinct peaks in March and May. Whilst it is obvious, therefore, that an important part of the breeding occurs at this time, it is uncertain whether the unsatisfactory data may merely be concealing the double spring peak which was so characteristic of the northern areas, or whether, in fact, breeding at this time may be truly more irregular, with a tendency to centre on the month of April. A similar consideration applies in the case of the October group, for there were double peaks (September and November or December) in 1932, 1933 and 1937.

Turning now to area J, it is clear that roughly the same grouping applies, although there is a distinct tendency for the summer breeding period to be later, *i.e.* with peaks of young stages in August or even September. There were again two spring peaks in 1937.

This problem can be approached in an alternative manner by ascertaining those periods in which the numbers of young stages exceed those of the later stages, and it is striking that just the same grouping is found, with just the same tendency for area J to be a little later in the summer and autumn. There is, therefore, fairly good reason to suppose that there tend to be three chief breeding periods in this region and not four, as there are to the north. Whilst this is a little surprising (in so far as one normally expects to find more breeding periods to the south of a region than to the north), it may possibly be accounted for by the relative dominance in the southern waters of "helgolandicus" (which, elsewhere, had typically two dominant peaks in the summer and autumn), in contrast to the dominance in the north of "finmarchicus" (with its two dominant spring peaks). For all that, and particularly in area H (dominantly a "finmarchicus" area in the first half of the year), the spring peak in the south is the major peak, although its relative dominance is very much less than that found in the chief spring peak of the northern areas.

It is noticeable that the first occurrences of significant numbers of young stages appear to fall into a distinct pattern, particularly in area H. They occurred (Text-fig. 18) a month earlier in each year from 1933 (or perhaps 1932) to 1935 (*i.e.* May, April, March), with a recurrence of the same feature from 1937 to 1939. Since the first appreciable number of young stages in 1936 occurred in June, there is, from 1936 to 1939, a sequence of some interest, and one which may perhaps be associated with a progressive change in the incidence of high salinity water in this region of the kind already noted by Wimpenny (1944).

[*Hull Bulletins of Marine Ecology, No. 15, Vol. II, pp. 277–281, Plates CIX–CXXIV, July, 1951.*]

CONTINUOUS PLANKTON RECORDS:

FISH EGGS AND YOUNG FISH IN THE NORTH SEA, 1932-39.

BY

H. G. STUBBINGS, M.A., Ph.D., B.Sc.

(*Editorial note.*—From the beginning of the Recorder Survey in 1932 an estimate was made of the total number of fish eggs and young fish in each sample. During 1940 and 1941 Dr. Stubbings undertook the extensive task of re-examining all the young fish caught between 1932 and 1939, and contrived, in spite of many technical difficulties, to identify the majority of them to genus and some to species. Dr. Stubbings then became engaged in research on pests in stored grain, and later took up a temporary war-time appointment with the Admiralty. However, before he left University College, Hull, he drafted an account of the distribution of the young fish and prepared a number of plates and text-figures which were sent to the printers. At the end of the war Dr. Stubbings resigned his post at University College, Hull, and remained in his Admiralty appointment. The young fish work was continued in turn by Mr. N. B. Marshall (now of the British Museum of Natural History), Mr. A. Saville (now of the Scottish Home Department, Marine Laboratory, Aberdeen), and recently by Dr. G. T. D. Henderson.

Further results from the extended survey which covers the northern North Sea and gives additional lines running into the Atlantic have added much to the information that was available to Dr. Stubbings; therefore it seems more useful to discuss the results from 1932 to 1939 and from 1946 to 1949 together in a single ‘ Bulletin,’ which is being prepared by Dr. Henderson. On the other hand certain lithographed plates showing the pre-war distributions of the eggs and larvae have already been printed, and these have been serially numbered as part of Volume II where, indeed, they logically belong for comparison with the other plankton taken during the same period. These completed plates are now presented with the bare minimum of explanation.

It should be stressed that Dr. Stubbings' contribution to the work is not restricted to the mere identification of the larvae. He gave the results much thought, and made constructive comments which will be incorporated in the later discussion. However, while many of his ideas can now be confirmed or amplified, some must be modified in the light of the subsequent data, and it is for this reason that a full discussion of them is reserved for a later ‘ Bulletin ’ in Vol. III.)

EXPLANATION.

The fish eggs and young fish whose distributions are shown in Plates CIX to CXXIV were collected during the Plankton Recorder Survey of the North Sea during the years 1932 to 1939. The methods used and the scope of the survey have been described by Hardy (1939 and 1941). For the first five and a half years the Recorder routes were restricted to the southern North Sea, but from January, 1938, until August, 1939, when the war prevented further sampling, they covered an area extending northwards to a line from the Shetlands to Norway.

The use of the non-committal term "young fish" is intentional, expressions such as "larvae," "post larvae" and "fry" being avoided; it covers all the stages collected by the Recorder from newly hatched larvae with their yolksacs to those about to metamorphose or, in a few cases, in the process of doing so.

The identification of the material presented a number of problems. It is inevitable in the Recorder method that the larger plankton organisms are squashed between the "catching" and "covering" silks as they wind on to the storage spool; before the fusee mechanism and the folded edges of the covering silk were introduced (Hardy, 1939, p. 25) the effect of the crushing was very considerable. Practically all specimens were to some extent mutilated and had imprinted upon them the pattern of the silk mesh, so that the chromatophore arrangement was obscured. Although the later material which had been stored while still on the silk was in far better condition than the earlier which had been scraped off, it seemed that little would be achieved by attempting identification beyond genus. Over the whole period 73% of the specimens could be assigned to genera and a further 8% to species, leaving 19% unidentifiable. It is thought that these latter were mostly gadoids and pleuronectids.

The following is a list of all species identified during the survey. A few other unidentified species were recorded.

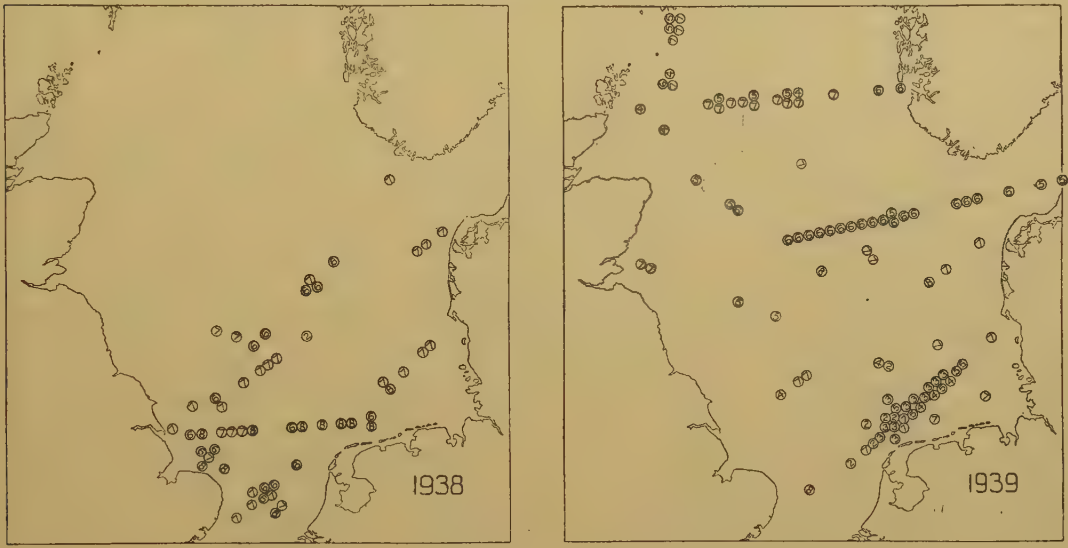
Trachurus trachurus (Linn.).
Trachinus vipera (Cuv. et Val.).
Gobius niger (Linn.).
Callionymus lyra (Linn.).
Solea vulgaris (Quensel).
Solea lutea (Bp.).
Pleuronectes limanda (Linn.).
Pleuronectes platessa (Linn.).
Pleuronectes flesus (Linn.).
Pleuronectes microcephalus (Donov.).
Pleuronectes cynoglossus (Linn.).
Arnoglossus laterna (Willoughby).
Rhombus maximus (Linn.).
Gadus aeglefinus (Linn.).
Gadus callarias (Linn.).
Gadus merlangus (Linn.).
Gadus poutassou (Risso).
Gadus virens (Linn.).
Onos cimbrius (Linn.).
Onos mustela (Linn.).
Brosmius brosme (Asc.).
Ammodytes spp.
Clupea harengus (Linn.).
Clupea sprattus (Linn.).
Anguilla anguilla (Linn.).

Of these only the genera *Pleuronectes*, *Gadus*, *Ammodytes* and *Clupea* occurred with any regularity, or in any abundance.

An analysis of the total number of specimens caught on the three southern lines during the period of the survey shows that the commoner genera occur in the following proportions :

Ammodytes spp.	34·4%	*Pleuronectes spp.*	4·3%
Clupea spp.	20·6%	Other spp.	3·1%
Gadus spp.	18·3%	Unidentifiable	19·3%

Of the *Clupea* spp. it is known that *Clupea harengus* was much the commoner in these records. Of the young gadoids, *Gadus aeglefinus* was the most often identified, followed by *Gadus merlangus* and *Gadus callarias*, about one-half and one-third as frequently respectively. Fewer pleuronectids were assigned to species, and of these *Pleuronectes platessa* was the most frequent.



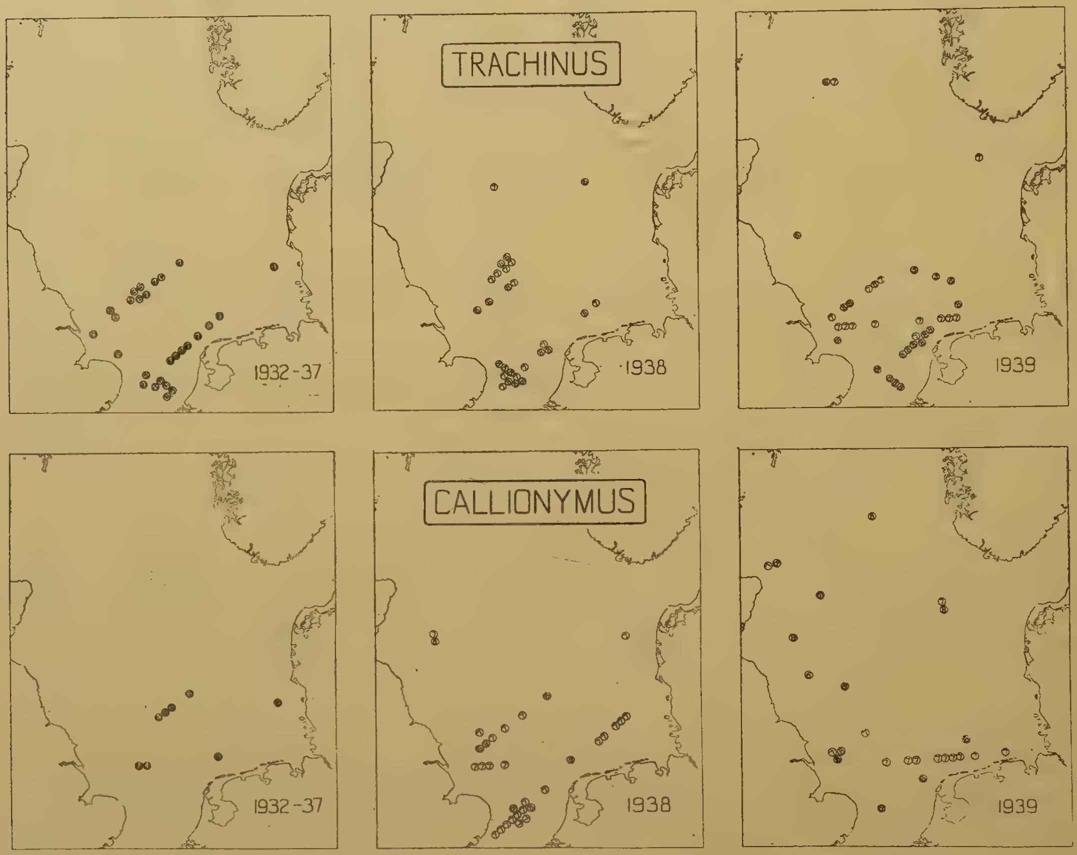
TEXT-FIG. 1.—Charts showing the positions at which young *Gadus merlangus* were taken during 1938–39. The numerals in the circles represent the month: 2 = February, 7 = July, etc.

The fish eggs, because of the crushing and the subsequent storage in formalin, were in the main beyond identification, although a proportion of them on a size basis alone could be attributed to plaice.

All samples were taken at one depth, 10 metres below the surface. The sample or " block " used throughout is equivalent to 10 miles of Recorder tow with a $\frac{1}{2}$-in. square aperture in the nose of the machine, which gives a theoretical volume of 3 cu. metres of water filtered. Prior to May, 1937, a $\frac{3}{4}$-in. square aperture was used and the silk was wound more slowly through the machine, (Hardy, 1939,

p. 41). The earlier results, however, have been adjusted to conform to the later ones, when a ½-in. square aperture was used.

The present object is to make the basic data available for discussion in a subsequent 'Bulletin,' and the material is restricted to a series of charts showing the distributions found in the various months. The fish eggs, all grouped into a single category, are shown on Plates CIX to CXI; few eggs were taken in the later months of each year and charts are only included for January to August. The total young fish, less those recognized as clupeids, are shown on Plates CXII to CXV and the *Clupea* on Plates CXVI, CXVII and CXX, with a summary on Plate CXV which takes the form of the average number of *Clupea* caught during the eight years on each 10-mile "block" in each month. *Ammodytes spp.* are arrranged in the same way as the *Clupea* on Plates CXVIII, CXIX, CXXI and CXXII.



TEXT-FIG. 2.—Charts showing the positions at which young *Trachinus* and *Callionymus* were taken during 1932 to 1939. The distribution from 1932–37 is shown on the left-hand chart in each case and the white numeral on a black circle indicates the year. On the other charts the black numeral in the circle indicates the month of occurrence: 5 = May, 8 = August, etc.

The distributions of the gadoids and pleuronectids are shown on Plates CXXIII and CXXIV, and Text-figs. 1 and 2 give a summary of the occurrences of *Gadus merlangus*, *Trachinus* and *Callionymus*.

As explained above, all discussion of the method and the implications of the results will be included in a ' Bulletin ' now being prepared, which will deal at the same time with the data derived from the post-war survey, between 1946 and 1949.

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EXPLANATION OF PLATES CIX–CXXIV.

PLATES CIX–CXI.

Charts showing the distribution of Fish Eggs from June, 1932 to July, 1939. Certain months, in which eggs were very scarce or absent, are omitted. Symbols denote the varying numbers per 10-mile block (see scale on Plate CIX). Where more than one record was obtained in any month all are shown, the earliest above, and the others bracketed together, in chronological order below. The dates of the several traverses are shown in circles on the right-hand side, except for 1938 and 1939, when all dates are omitted owing to lack of space. (These dates can be obtained from the " Station List " (Hardy, 1941, Plates I–V).)

Where two or more months have been combined in one chart the same procedure is adopted, but the parallel lines for the different months are not bracketed and the date is indicated on the right-hand side of each line.

PLATES CXII–CXIV.

Charts showing the monthly distribution of Total Young Fish less Clupea from 1932 to 1939. The mode of presentation is the same as for Plates CIX–CXI except that the later months in each year are combined; these never produced more than five fish per block, and such occurrences are indicated by the initial letters of the months (O, N and D) on the appropriate blocks. Data for August to December, 1938, and August, 1939, are shown on Plate CXV.

PLATE CXV.

A series of twelve charts showing graphically the average number of Young Clupea per block on each of the Southern North Sea lines (C, B, R and E) for each month over the period 1932–1939; also charts continuing the distribution of Total Young Fish less Clupea for August to December, 1938, and August, 1939, from Plate CXIV.

PLATES CXVI AND CXVII.

Charts showing the monthly distribution of Young Clupea from 1932 to 1937. The arrangement is similar to that for the Total Young Fish less Clupea (Plates CXII–CXIV), except that in October, 1935, the presence of numbers higher than five on the C line is denoted by the usual symbols. The data for 1938 and 1939 are shown on Plate CXX.

PLATES CXVIII AND CXIX.

Charts showing the monthly distribution of Young Ammodytes from 1932 to 1937. The arrangement is similar to that for Total Young Fish less Clupea (Plates CXII–CXIV). The data for 1938 and 1939 are shown on Plates CXXI and CXXII.

PLATE CXX.

Charts continuing the monthly distribution of Young Clupea for certain months in 1938 and 1939 from Plate CXVII. Numbers higher than five in May, 1938, and March and April, 1939, are denoted by the usual symbols.

PLATE CXXI.

Charts continuing the monthly distribution of Young Ammodytes for certain months in 1938 and 1939 from Plate CXIX. See also Plate CXXII.

PLATE CXXII.

A series of twelve charts showing graphically the Average Number of Young Ammodytes per block on each of the Southern North Sea lines (C, B, R and E) for each month over the period 1932–1939; also charts continuing the monthly distribution of Young Ammodytes from June to August, 1939.

PLATES CXXIII AND CXXIV.

Charts showing the distribution of Young Gadus (circles) and Pleuronectes (squares) from March to August for 1932 to 1939. Insignificant numbers were caught in the other months. In contrast to the previous plates of small charts, which are arranged to be read downwards, those in Plate CXXIII are arranged horizontally, the year being marked on the chart for the first month shown in each year.

FISH EGGS

PER BLOCK

• = 0
○ = 1-5
◯ = 6-10
⊕ = 11-25
◒ = 26-35
● = 36-50
◉ = >50

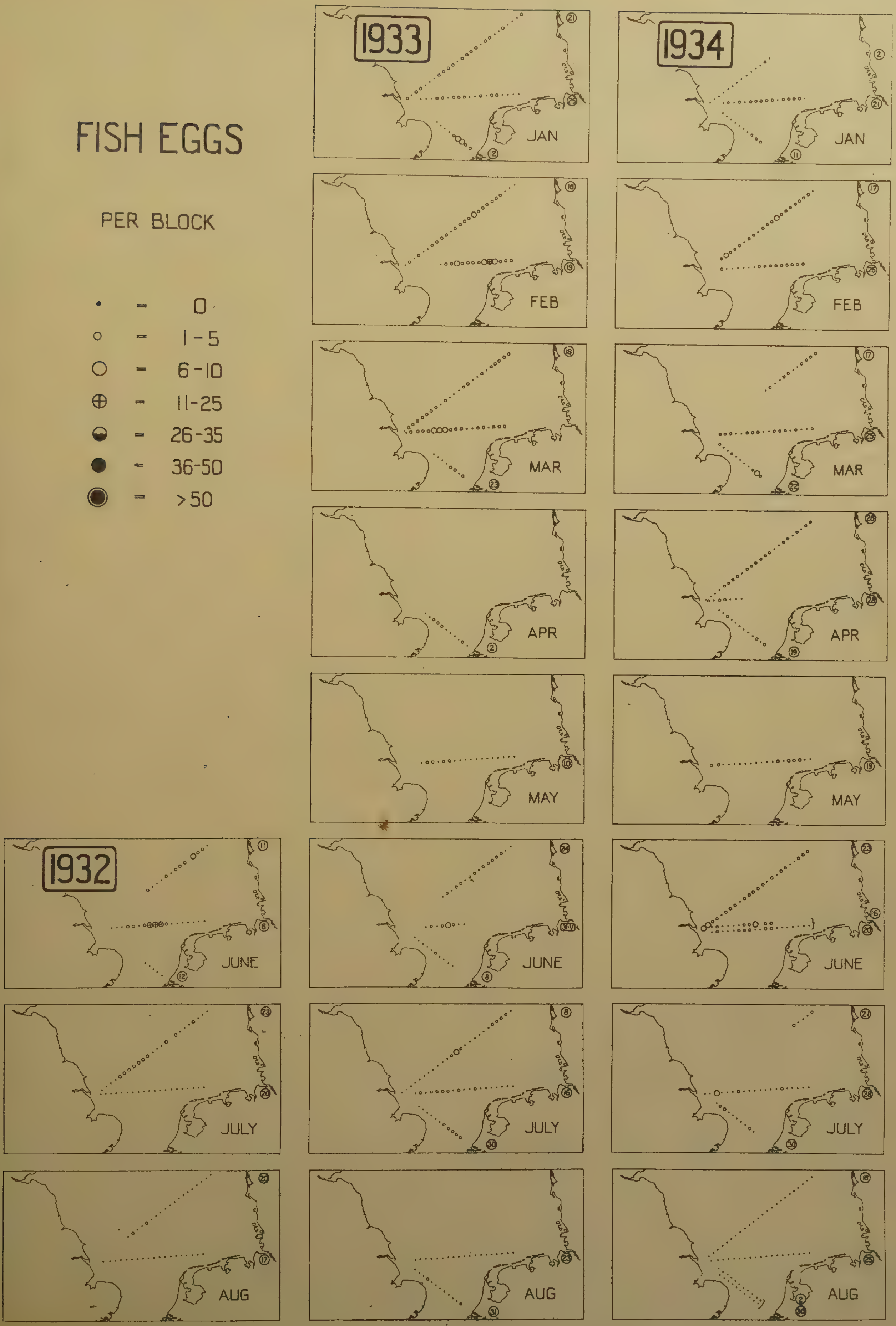
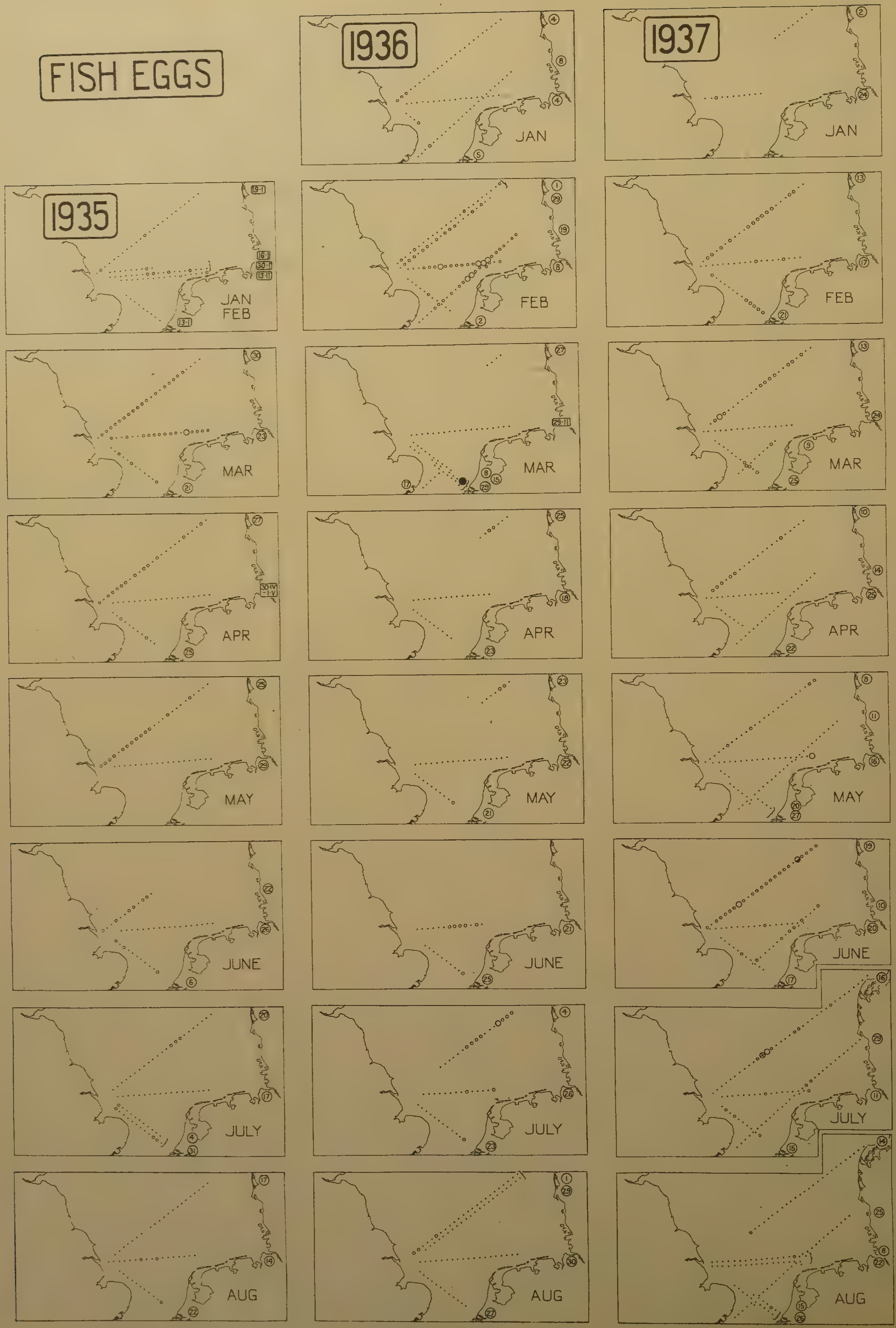

1933
1934
1932
JAN
JAN
FEB
FEB
MAR
MAR
APR
APR
MAY
MAY
JUNE
JUNE
JUNE
JULY
JULY
JULY
AUG
AUG
AUG

PLATE CX

FISH EGGS


1936
4
8
4
5
JAN
1937
2
24
JAN
1935
19·1
16·1
30·1
13·11
13·1
JAN
FEB
1
29
19
8
2
FEB
13
17
21
FEB
30
23
21
MAR
27
29·II
17
8
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MAR
13
24
9
25
MAR
27
30·IV
1·V
25
APR
25
18
23
APR
10
14
29
22
APR
25
29
MAY
23
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21
MAY
8
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27
MAY
22
26
6
JUNE
21
25
JUNE
19
10
20
17
JUNE
20
17
4
31
JULY
4
26
23
JULY
16
29
11
15
JULY
17
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22
AUG
1
29
30
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AUG
14
25
8
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15
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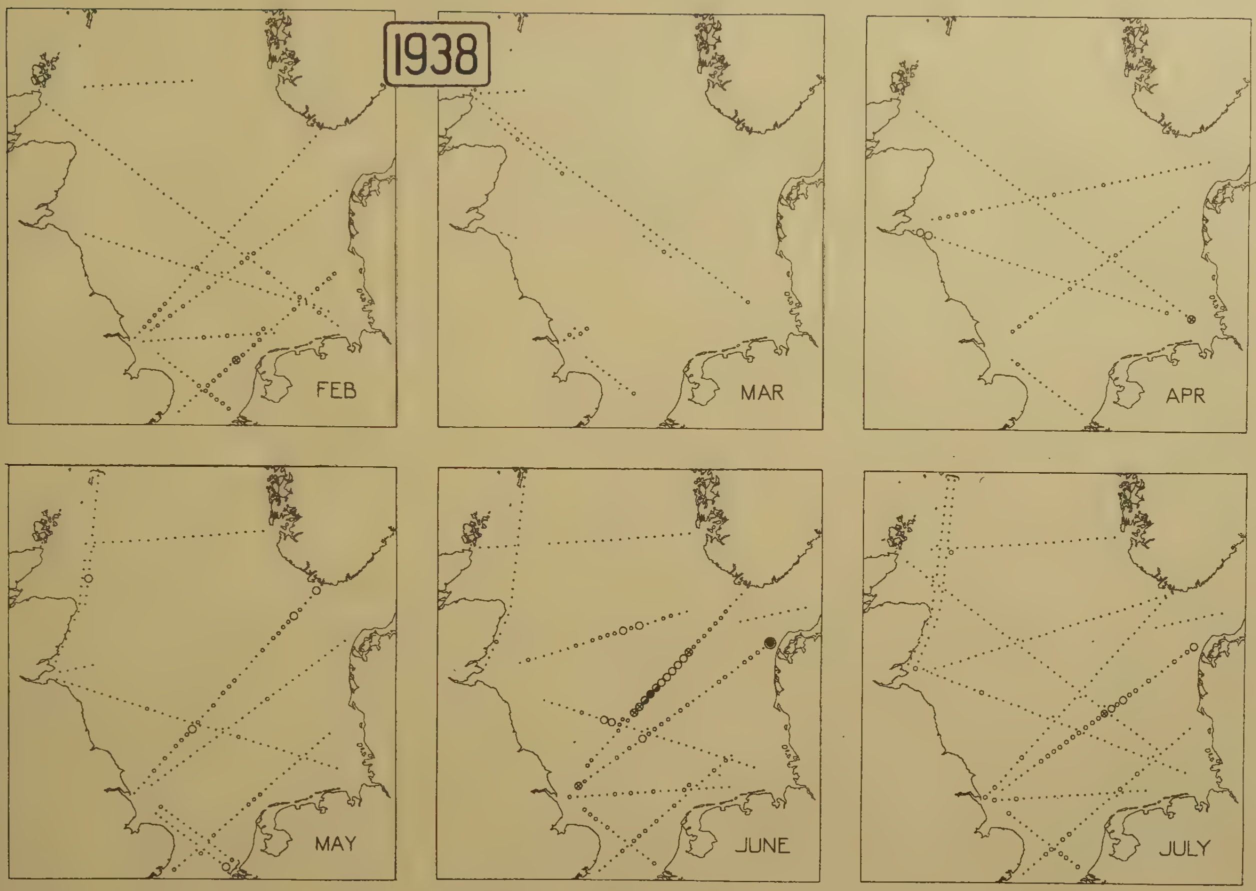
AUG

PLATE CXI


1938
FEB
MAR
APR
MAY
JUNE
JULY

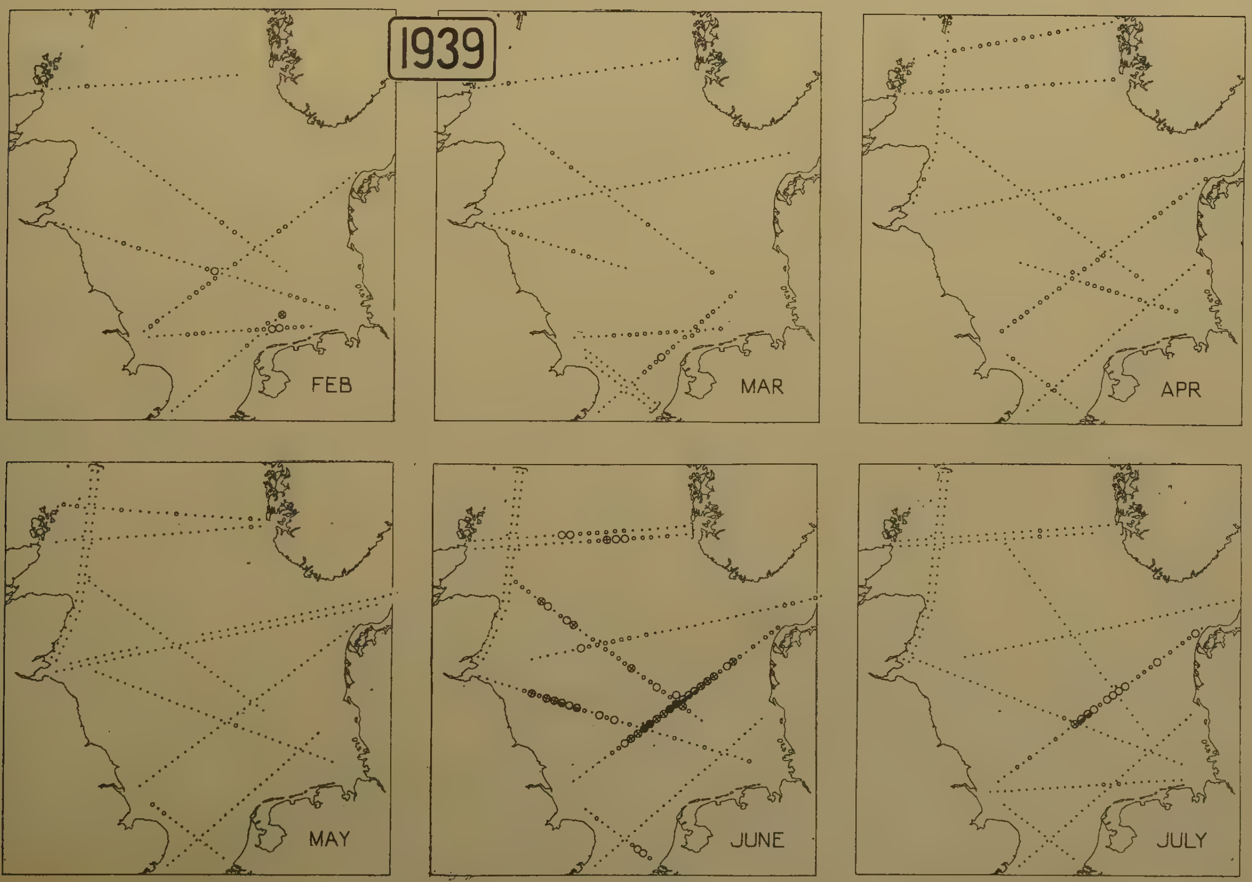
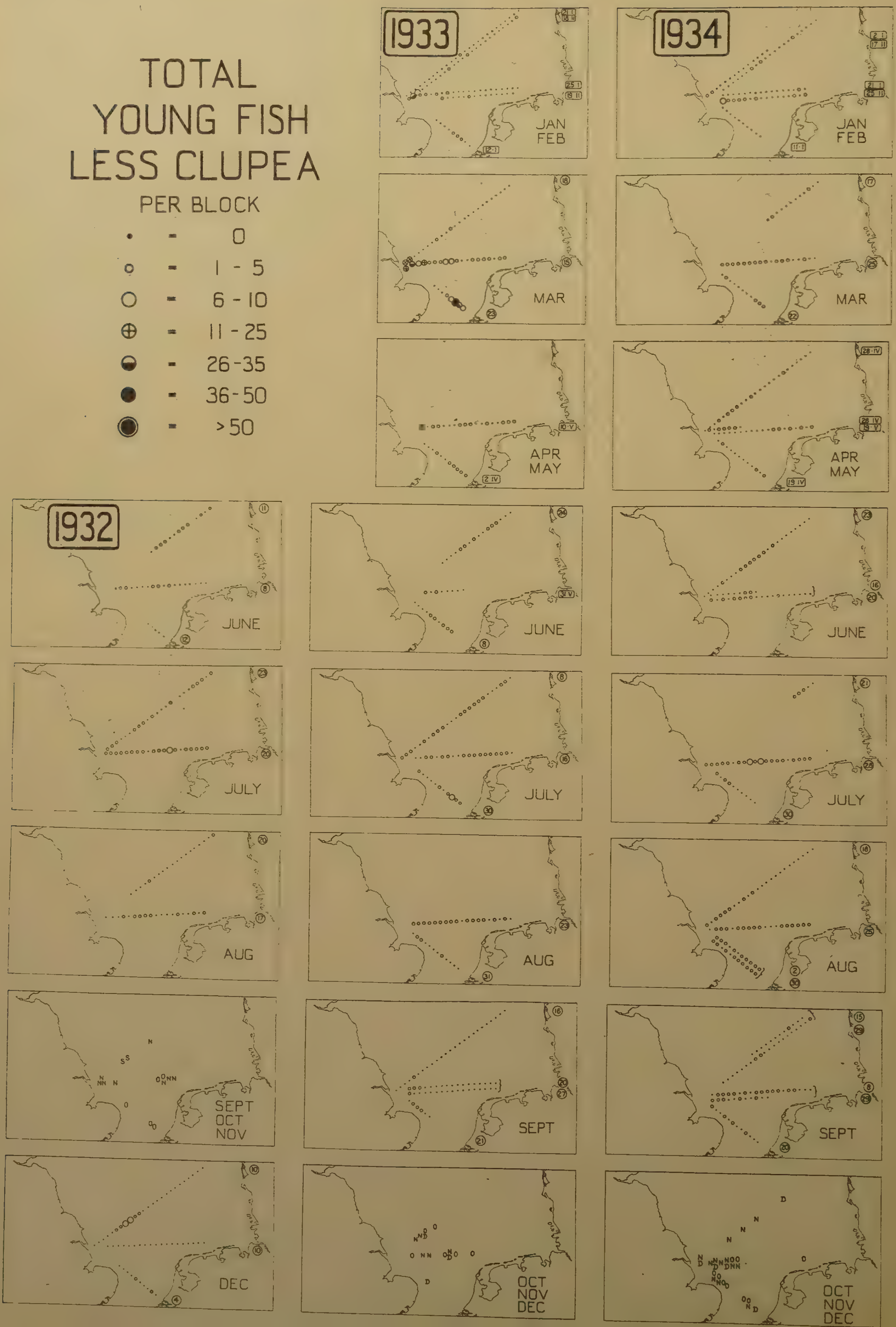

1939
FEB
MAR
APR
MAY
JUNE
JULY

PLATE CXII

TOTAL YOUNG FISH LESS CLUPEA

PER BLOCK

•	-	0
o	-	1 - 5
○	-	6 - 10
⊕	-	11 - 25
◒	-	26-35
●	-	36-50
◉	-	>50


1933
JAN FEB
MAR
APR MAY
1934
JAN FEB
MAR
APR MAY
1932
JUNE
JUNE
JUNE
JULY
JULY
JULY
AUG
AUG
AUG
SEPT OCT NOV
SEPT
SEPT
DEC
OCT NOV DEC
OCT NOV DEC

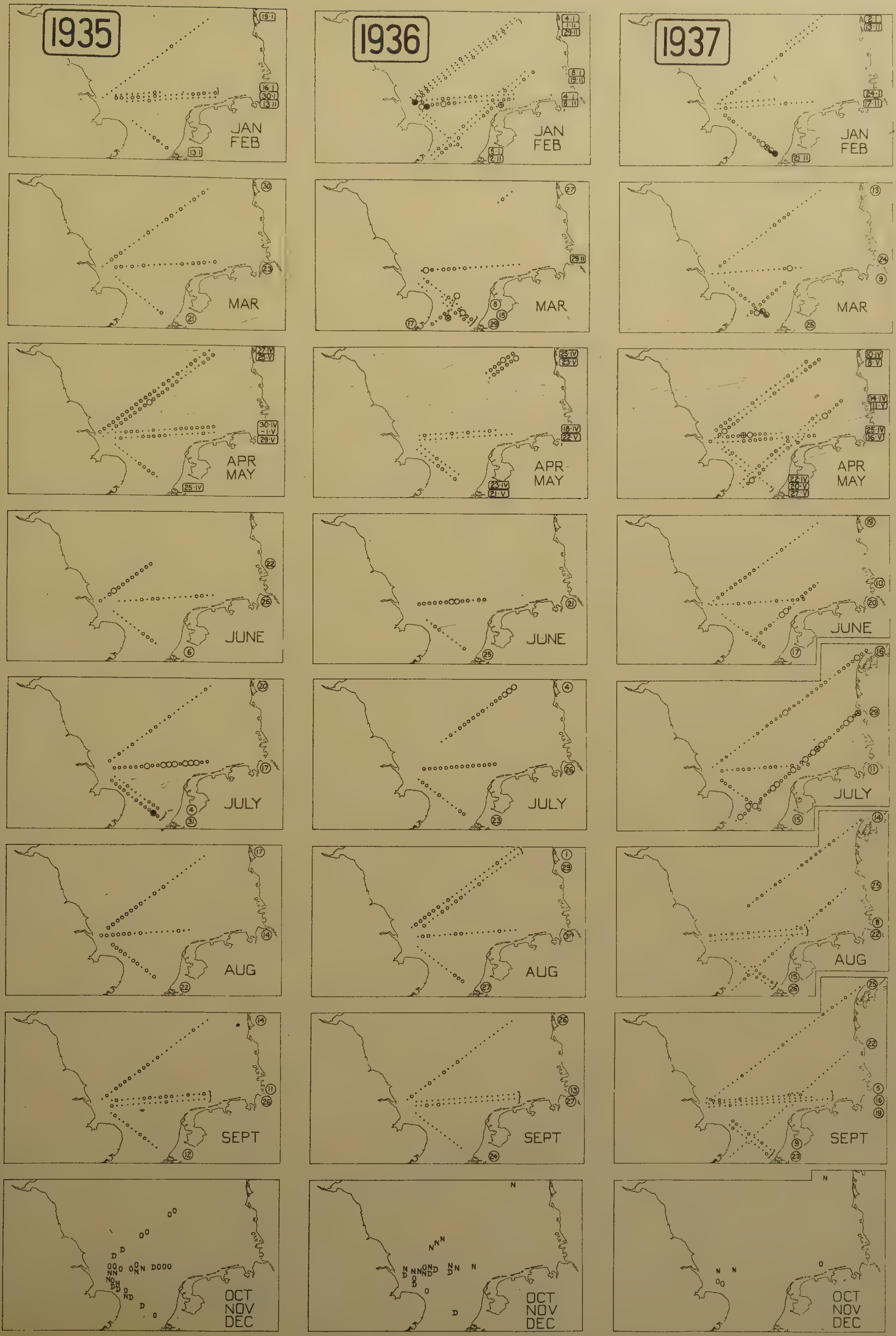
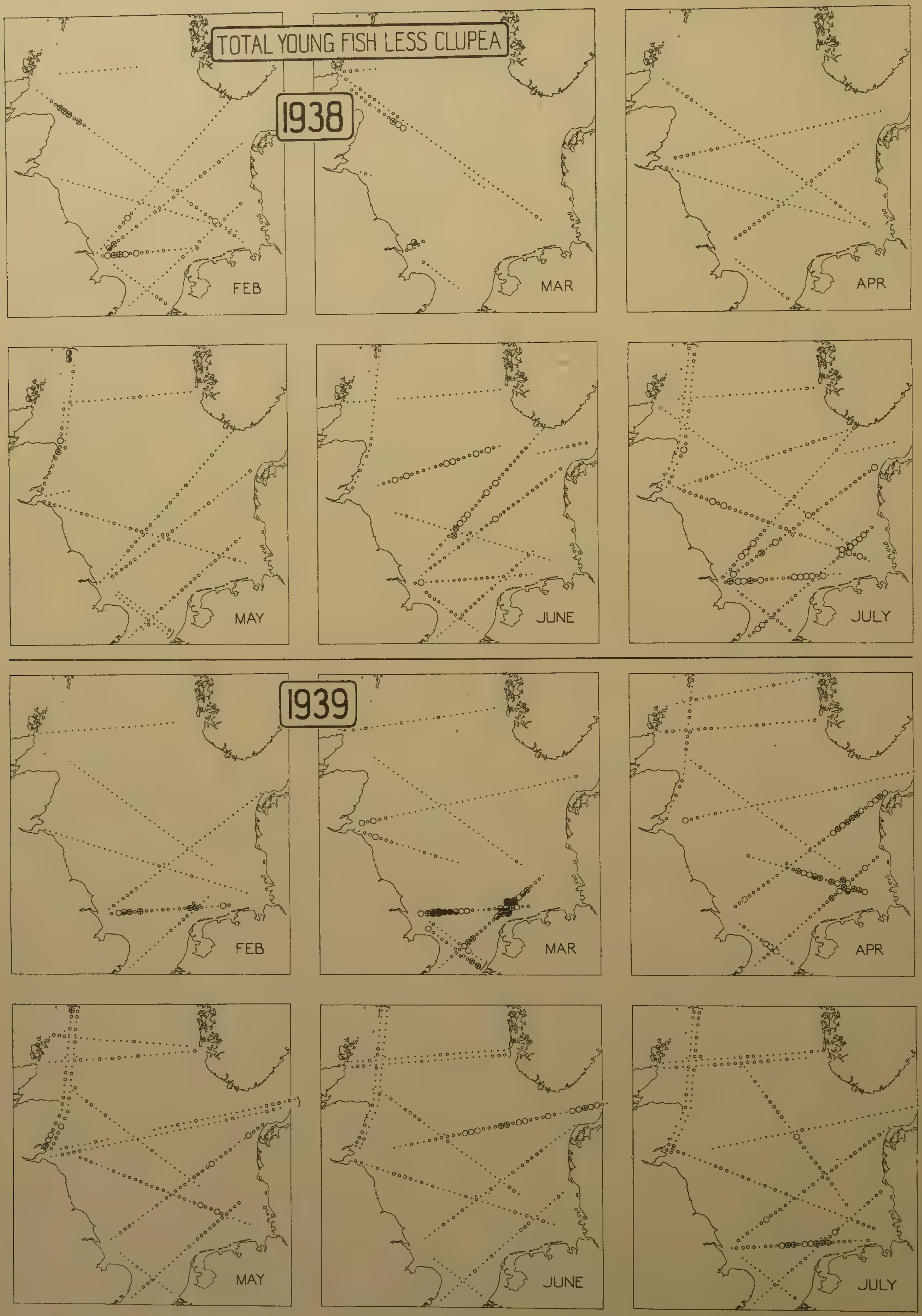
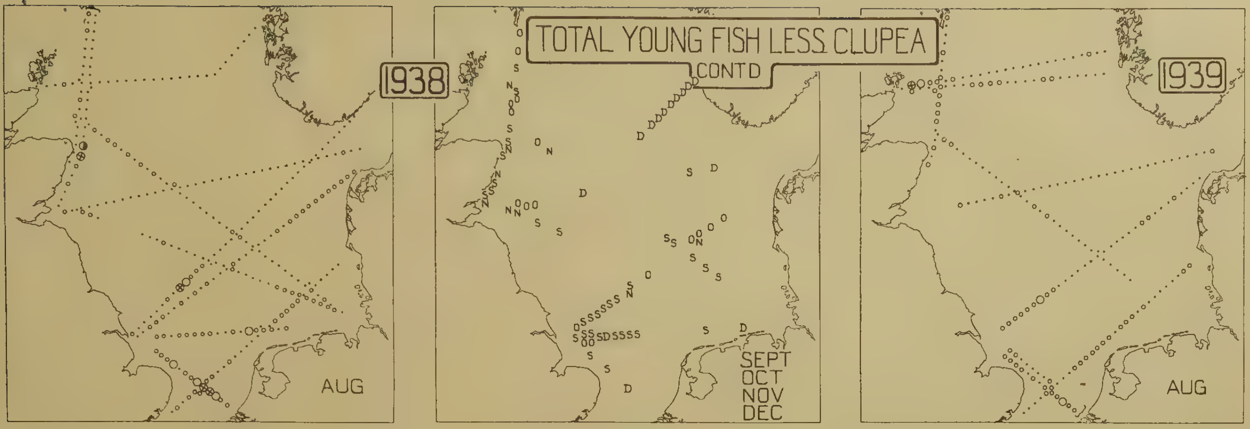

1935
19·I
16·I
30·I
13·II
13·I
JAN FEB
1936
4·I
1·II
29·II
8·I
19·II
4·I
8·II
5·I
2·II
JAN FEB
1937
2·I
13·II
24·I
17·II
21·II
JAN FEB
30
23
21
MAR
27
29·II
8
15
17
29
MAR
13
24
9
25
MAR
27·IV
25·V
30·IV
-1·V
29·V
25·IV
APR MAY
25·IV
23·V
18·IV
22·V
23·IV
21·V
APR MAY
10·IV
8·V
14·IV
11·V
25·IV
16·V
22·IV
20·V
27·V
APR MAY
22
26
6
JUNE
21
25
JUNE
19
10
20
17
JUNE
20
17
4
31
JULY
4
26
23
JULY
15
29
11
15
JULY
17
14
22
AUG
1
29
31
27
AUG
14
25
8
22
15
26
AUG
14
11
26
12
SEPT
26
13
27
24
SEPT
25
22
5
16
19
9
23
SEPT
OCT NOV DEC
OCT NOV DEC
OCT NOV DEC

PLATE CXIV


TOTAL YOUNG FISH LESS CLUPEA

1938
FEB
MAR
APR
MAY
JUNE
JULY
1939
FEB
MAR
APR
MAY
JUNE
JULY


1938
TOTAL YOUNG FISH LESS CLUPEA
CONTD
1939
AUG
SEPT
OCT
NOV
DEC
AUG

CLUPEA: AVERAGE NUMBER PER BLOCK FOR EACH MONTH 1932-39

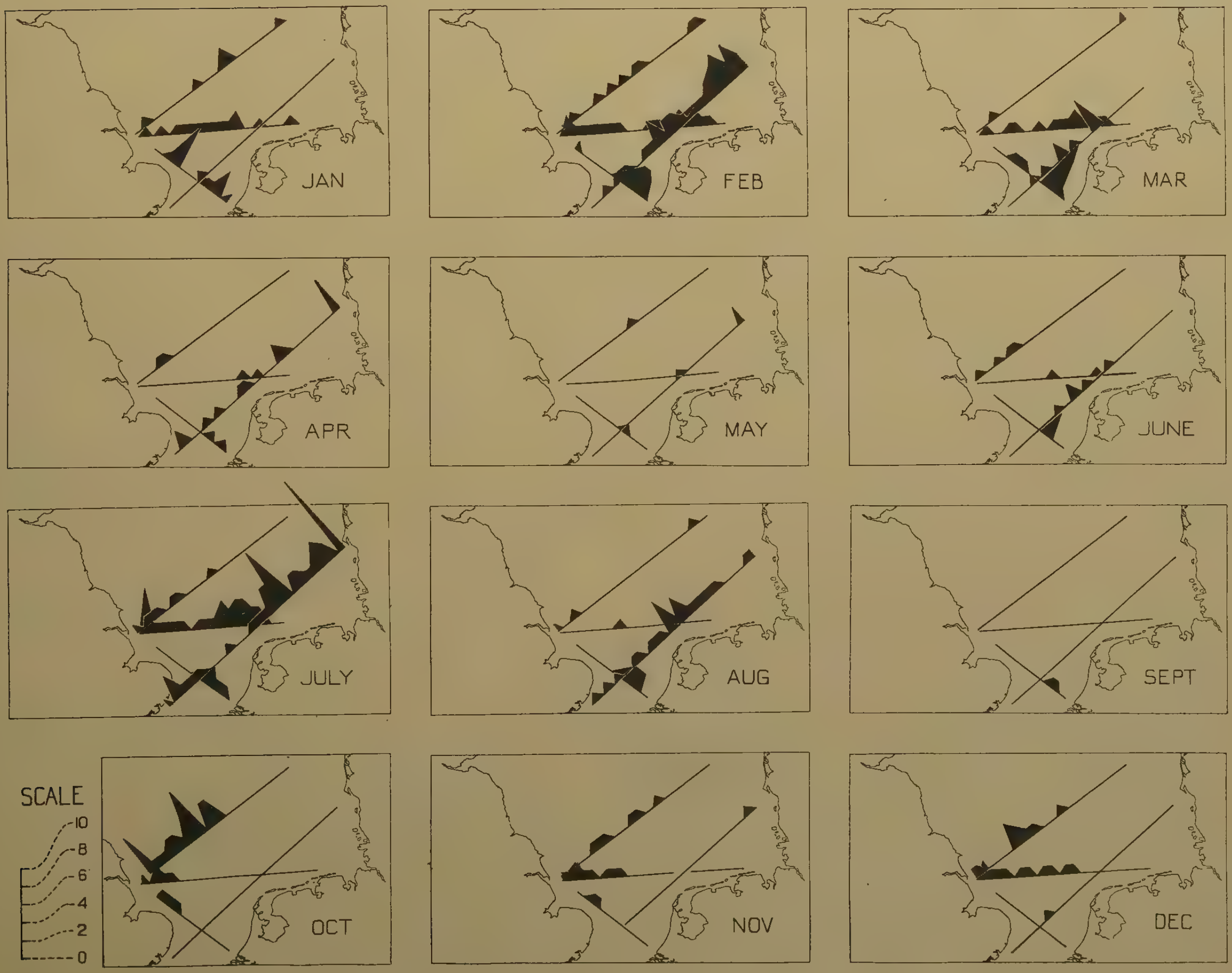
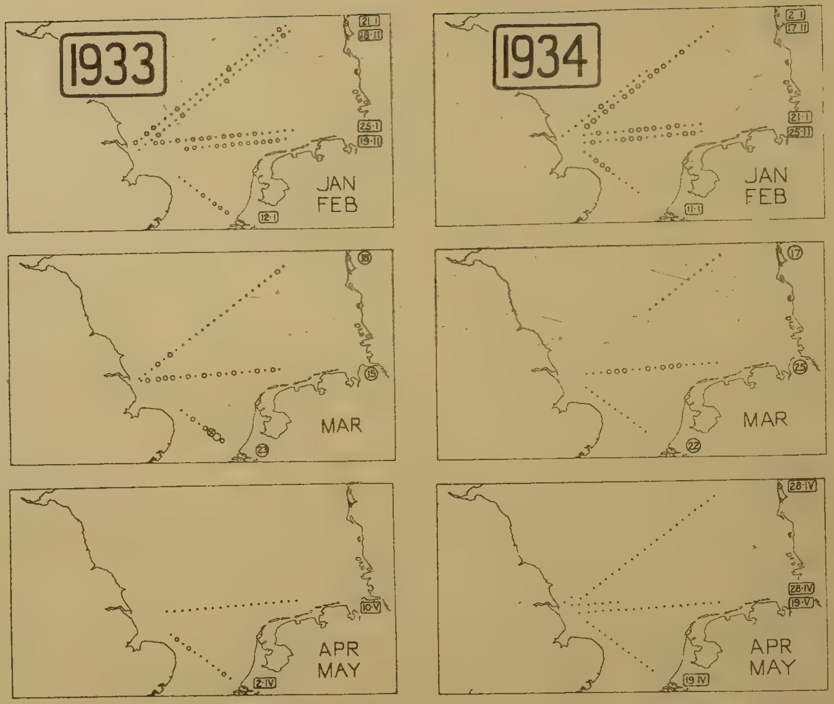

JAN
FEB
MAR
APR
MAY
JUNE
JULY
AUG
SEPT
SCALE
10
8
6
4
2
0
OCT
NOV
DEC

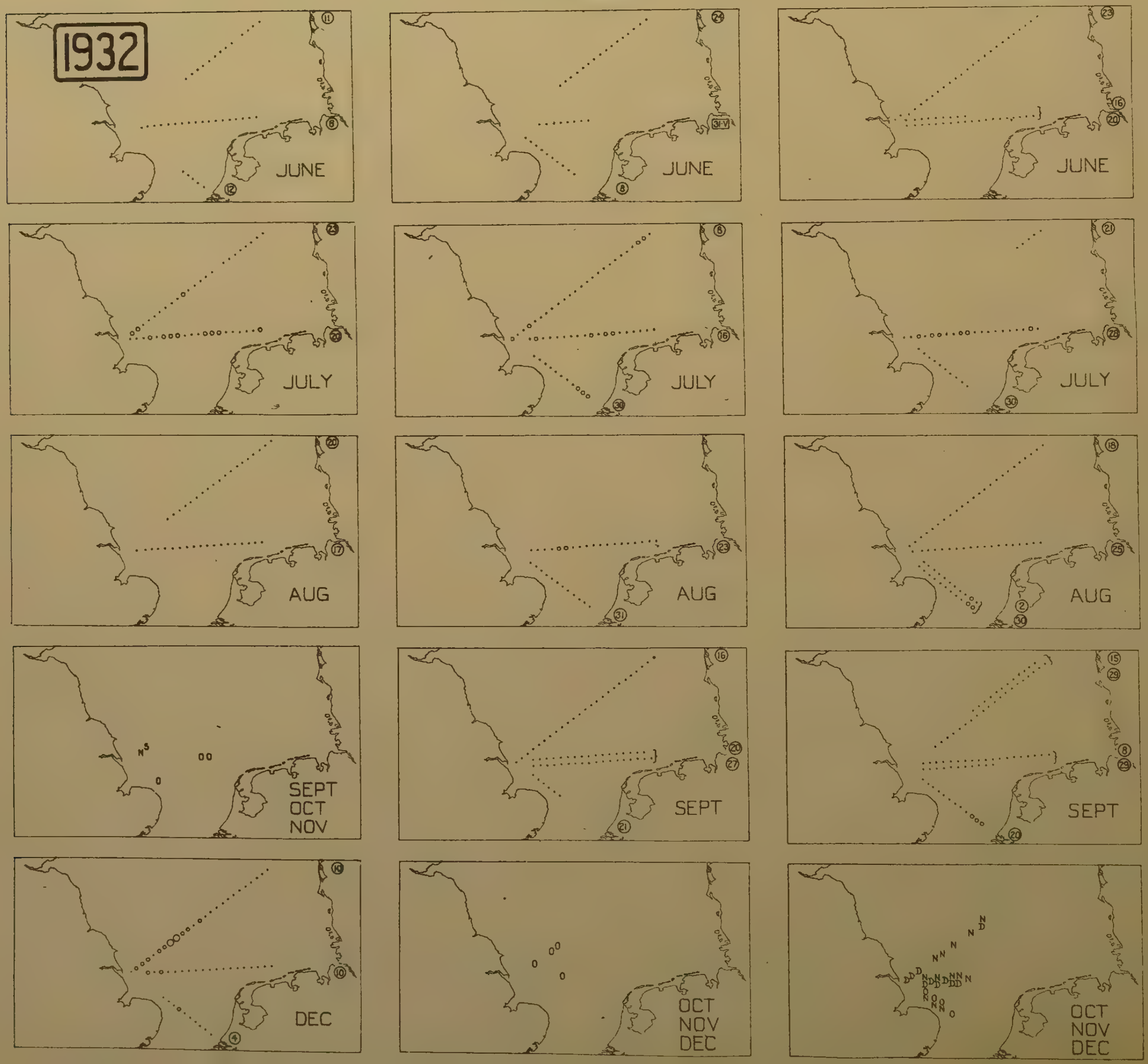
PLATE CXVI

CLUPEA

SCALE
PER BLOCK

·	=	0
○	=	1 - 5
◯	=	6 - 10
⊕	=	11 - 20
◒	=	21 - 36
●	=	36 - 50
⬤	=	> 50


1933
21 I
26 II
25 I
19 II
12 I
JAN
FEB
1934
2 I
17 II
21 I
25 II
11 I
JAN
FEB
18
15
23
MAR
17
25
22
MAR
10 V
2 IV
APR
MAY
28 IV
28 IV
19 V
19 IV
APR
MAY


1932
11
8
12
JUNE
24
31 V
8
JUNE
23
16
20
JUNE
23
30
JULY
8
16
30
JULY
21
28
30
JULY
20
17
AUG
23
31
AUG
18
25
2
30
AUG
SEPT
OCT
NOV
16
20
27
21
SEPT
15
29
8
29
20
SEPT
10
10
4
DEC
OCT
NOV
DEC
OCT
NOV
DEC

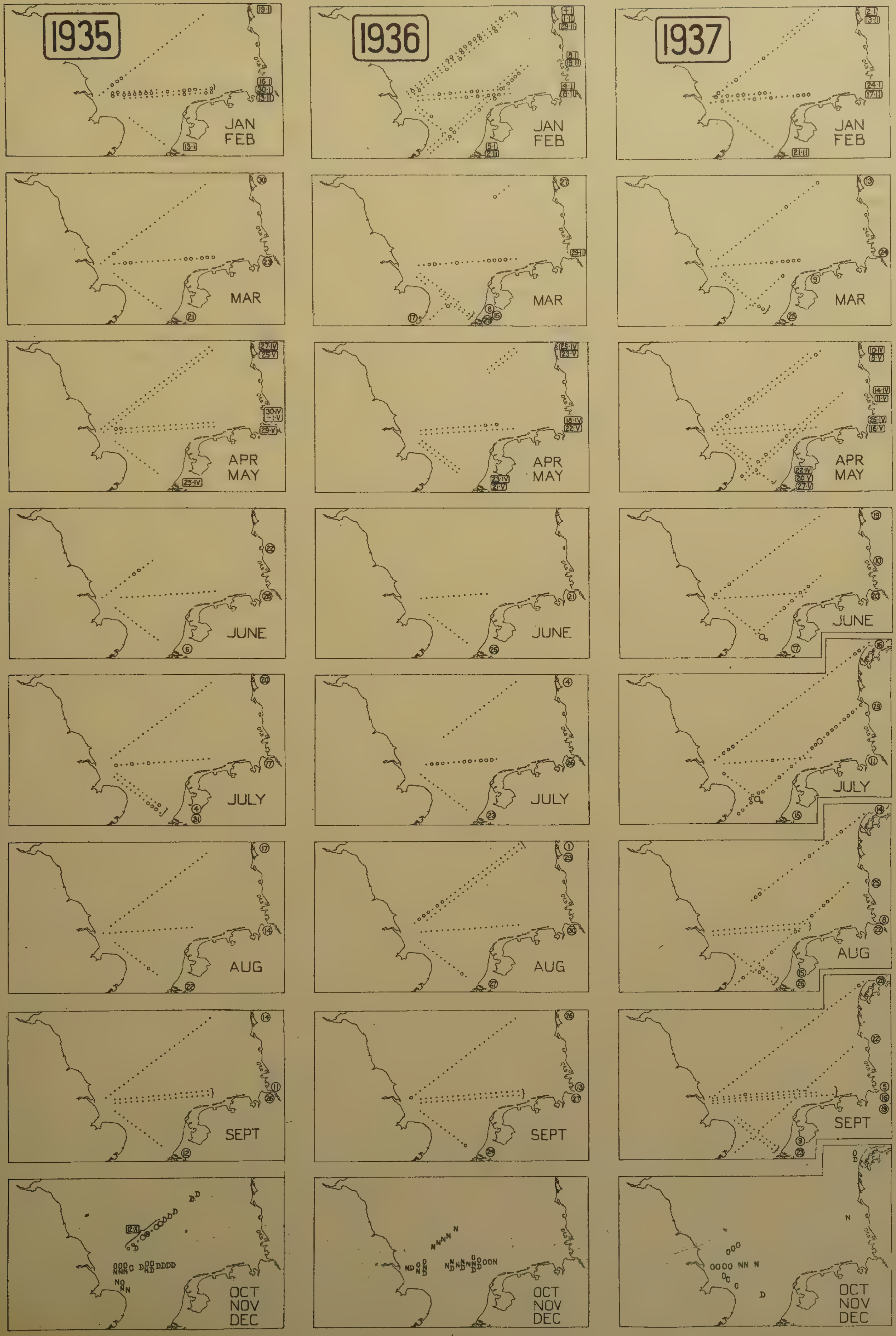
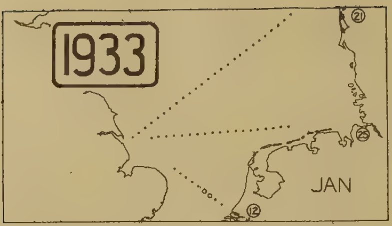

1935
19·I
16·I
30·I
13·II
13·I
JAN FEB
1936
4·I
1·II
29·II
8·I
15·II
4·I
6·II
5·I
2·II
JAN FEB
1937
2·I
13·II
24·I
17·II
21·II
JAN FEB
㉚
㉓
㉑
MAR
㉗
29·II
⑰
⑧
⑮
㉙
MAR
⑬
㉔
⑨
㉕
MAR
27·IV
25·V
30·IV –1·V
29·V
25·IV
APR MAY
25·IV
23·V
18·IV
22·V
23·IV
21·V
APR MAY
10·IV
8·V
14·IV
11·V
25·IV
16·V
22·IV
20·V
27·V
APR MAY
㉒
㉖
⑥
JUNE
㉑
㉕
JUNE
⑲
⑩
⑳
⑰
JUNE
⑳
⑰
④
㉛
JULY
④
㉖
㉓
JULY
⑯
㉘
⑪
⑮
JULY
⑰
⑭
㉒
AUG
①
㉙
㉚
㉗
AUG
⑭
㉕
⑧
㉒
⑮
㉖
AUG
⑭
⑪
㉖
⑫
SEPT
㉖
⑬
㉗
㉔
SEPT
㉘
㉒
⑤
⑯
⑲
⑨
㉓
SEPT
12·X
OCT NOV DEC
OCT NOV DEC
OCT NOV DEC

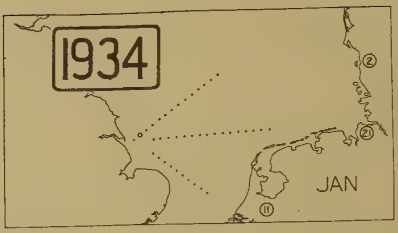
PLATE CXVIII

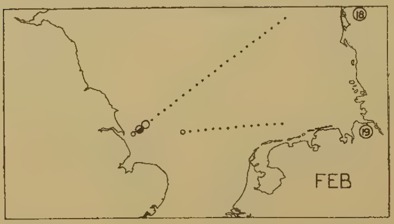
AMMODYTES
Spp.

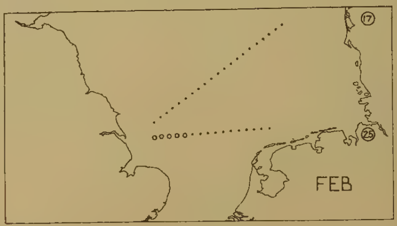
SCALE
PER BLOCK

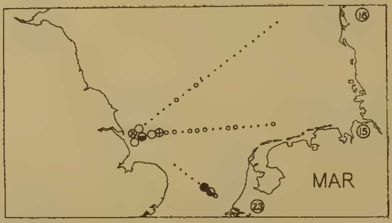
• - 0
∘ - 1-5
○ - 6-10
⊕ = 11-20
◒ - 21-36
● - 36-50
⬤ = >50

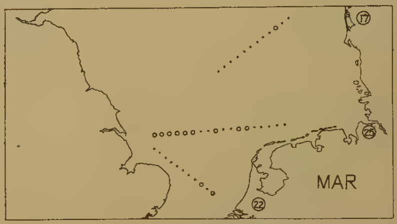

1933
㉑
㉕
⑫
JAN

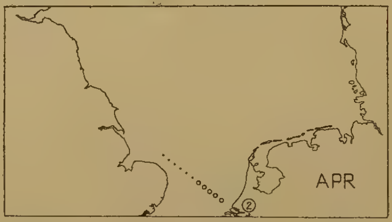

1934
②
㉑
⑪
JAN

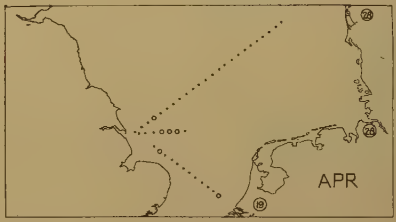


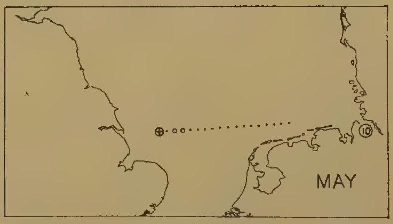


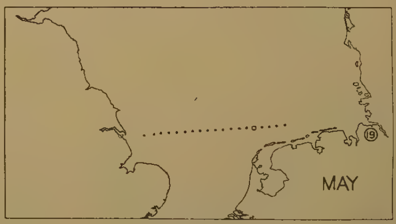


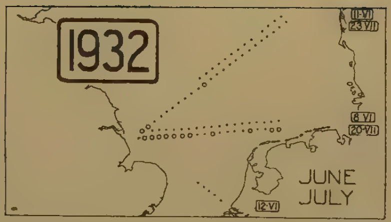


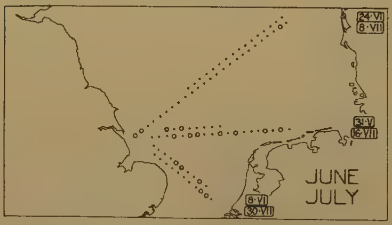


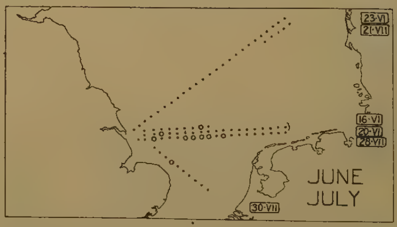


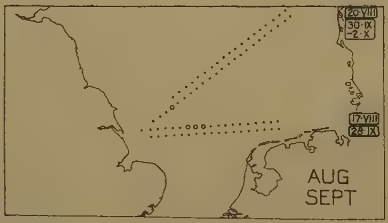


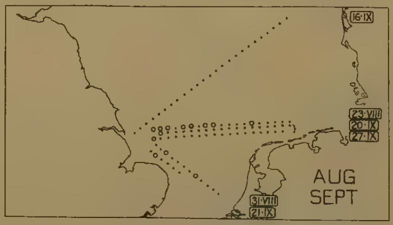


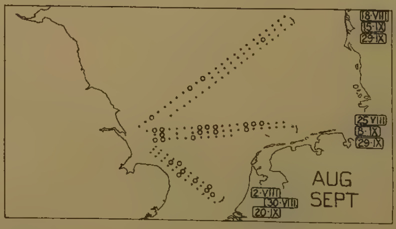

1932
11·VI
23·VII
8·VI
20·VII
12·VI
JUNE
JULY

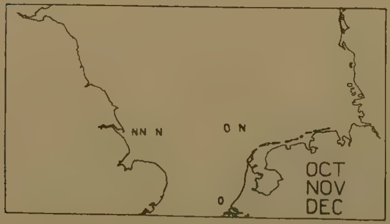

24·VI
8·VII
31·V
16·VII
8·VI
30·VII
JUNE
JULY

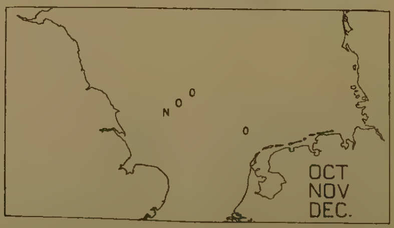

23·VI
21·VII
16·VI
20·VI
28·VII
30·VII
JUNE
JULY

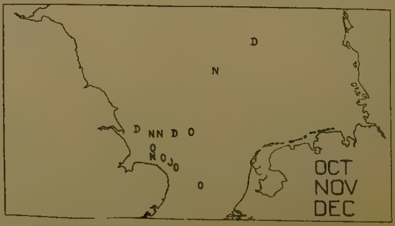

20·VIII
30·IX
-2·X
17·VIII
28·IX
AUG
SEPT


16·IX
23·VIII
20·IX
27·IX
31·VIII
21·IX
AUG
SEPT


18·VIII
15·IX
29·IX
25·VIII
8·IX
29·IX
2·VIII
30·VIII
20·IX
AUG
SEPT


NN N
O N
O
OCT
NOV
DEC


N O O
O
OCT
NOV
DEC.


D
N
D NN D O
O
N O
O
O
OCT
NOV
DEC

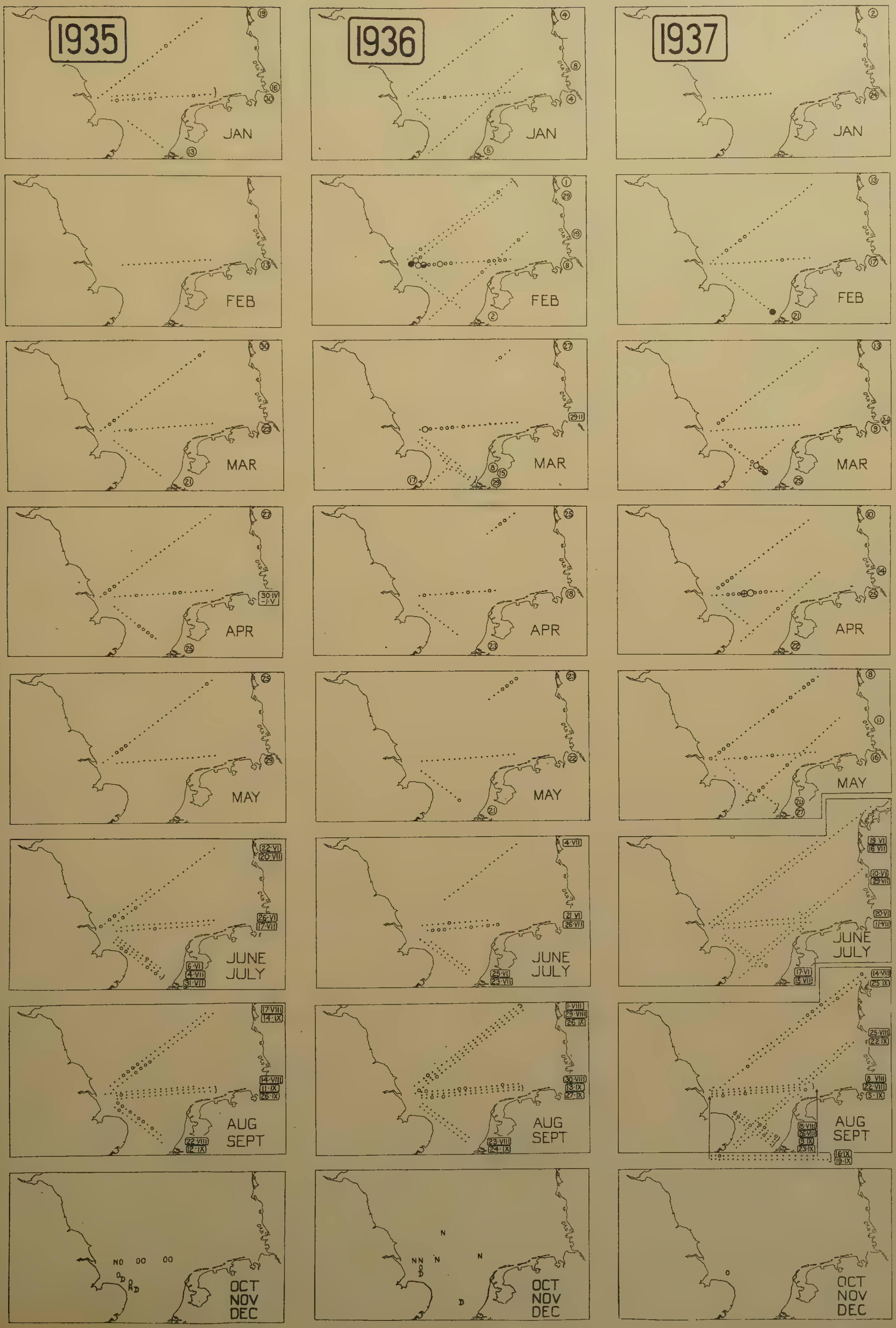

1935
1936
1937
JAN
FEB
MAR
APR
MAY
JUNE JULY
AUG SEPT
OCT NOV DEC
19
16
30
13
4
8
4
5
2
24
13
1
29
19
8
2
13
17
21
30
29
21
27
29·II
8
15
29
17
13
24
9
25
27
30·IV -1·V
25
25
18
23
10
14
25
22
25
29
23
22
21
8
11
16
20
27
22·VI 20·VII
26·VI 17·VII
6·VI 4·VII 31·VII
4·VII
21·VI 26·VII
25·VI 23·VII
19·VI 16·VII
10·VI 29·VII
20·VI 11·VII
17·VI 15·VII
17·VIII 14·IX
14·VIII 11·IX 26·IX
22·VIII 12·IX
1·VIII 29·VIII 26·IX
30·VIII 13·IX 27·IX
23·VIII 24·IX
14·VIII 25·IX
25·VIII 22·IX
8·VIII 22·VIII 5·IX
5·VIII 26·VIII 9·IX 23·IX
16·IX 19·IX

PLATE CXX

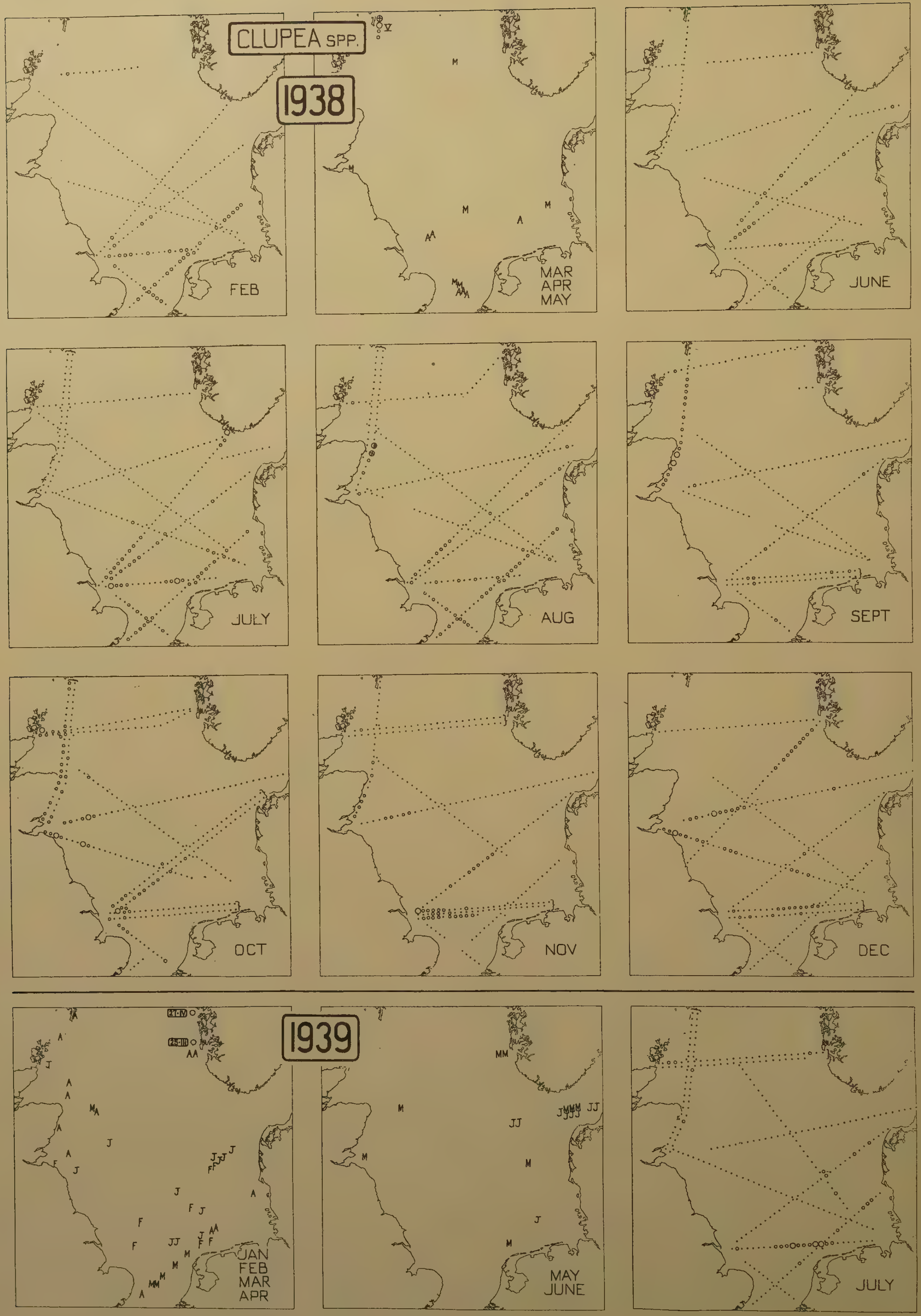

CLUPEA SPP.
1938
FEB
MAR
APR
MAY
JUNE
JULY
AUG
SEPT
OCT
NOV
DEC
1939
27·IV
25·III
JAN
FEB
MAR
APR
MAY
JUNE
JULY

PLATE CXXI

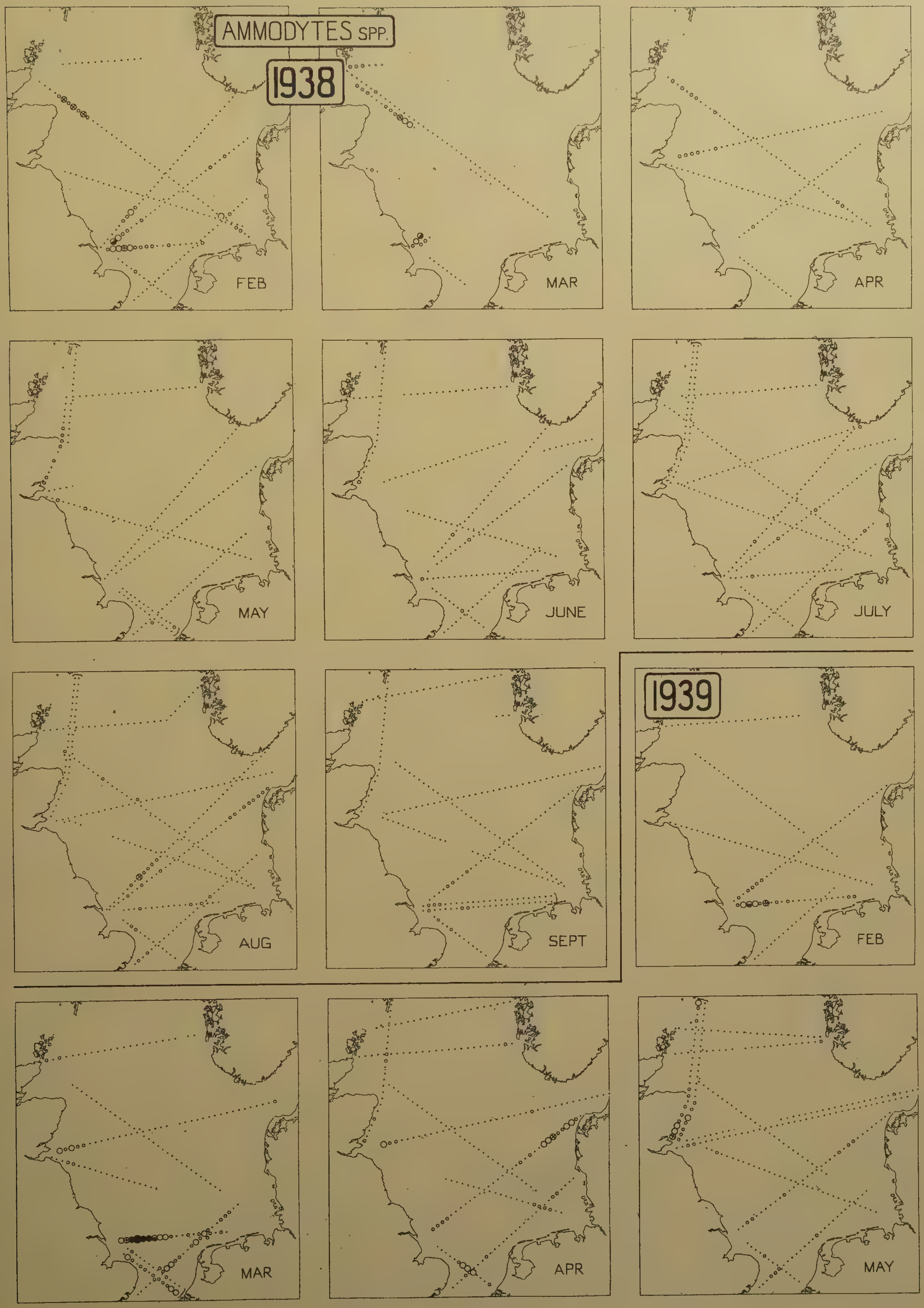
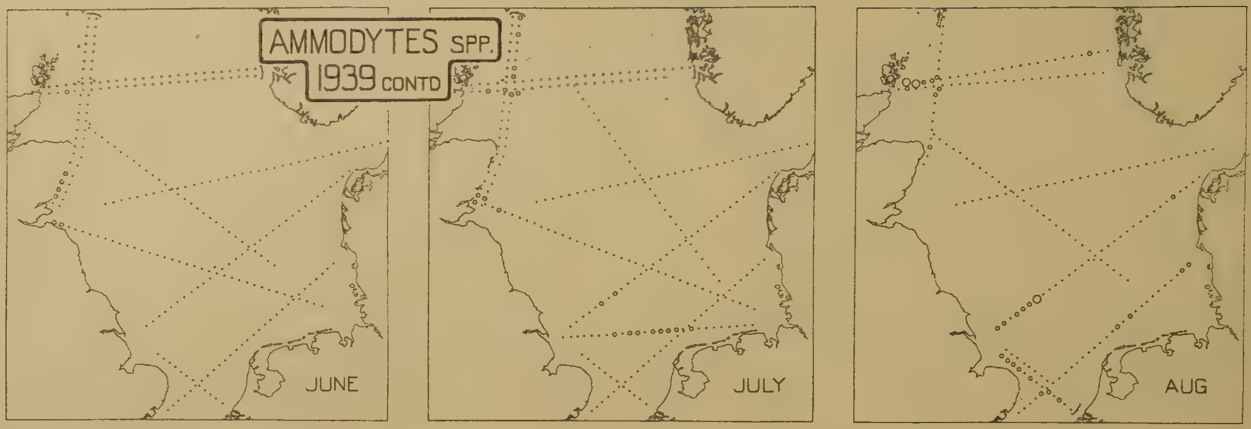

AMMODYTES SPP.
1938
FEB
MAR
APR
MAY
JUNE
JULY
AUG
SEPT
1939
FEB
MAR
APR
MAY

PLATE CXXII


AMMODYTES SPP.
1939 CONTD
JUNE
JULY
AUG

AMMODYTES: AVERAGE NUMBER PER BLOCK FOR EACH MONTH 1932-39

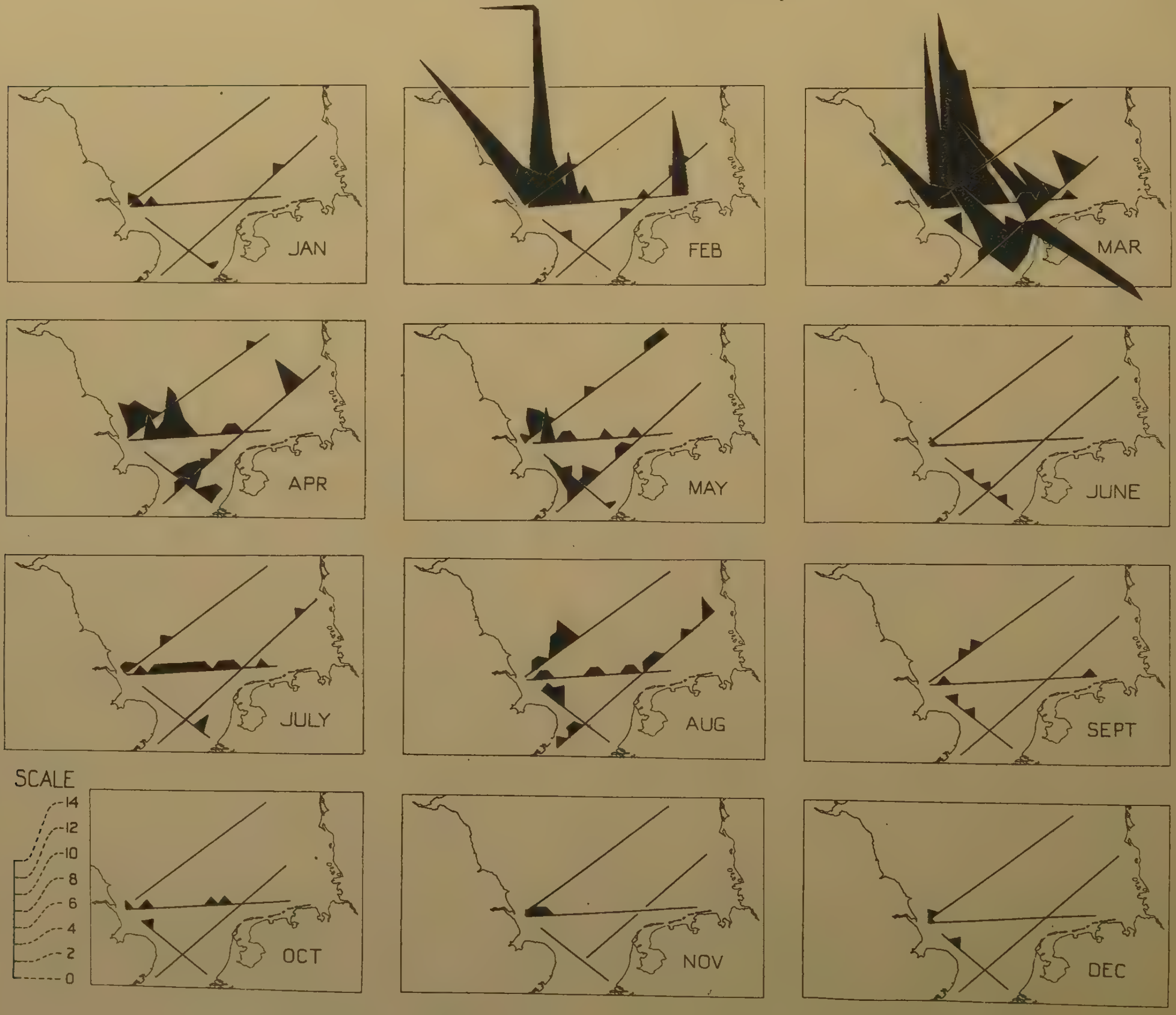

JAN
FEB
MAR
APR
MAY
JUNE
JULY
AUG
SEPT
SCALE
14
12
10
8
6
4
2
0
OCT
NOV
DEC

PLATE CXXIII

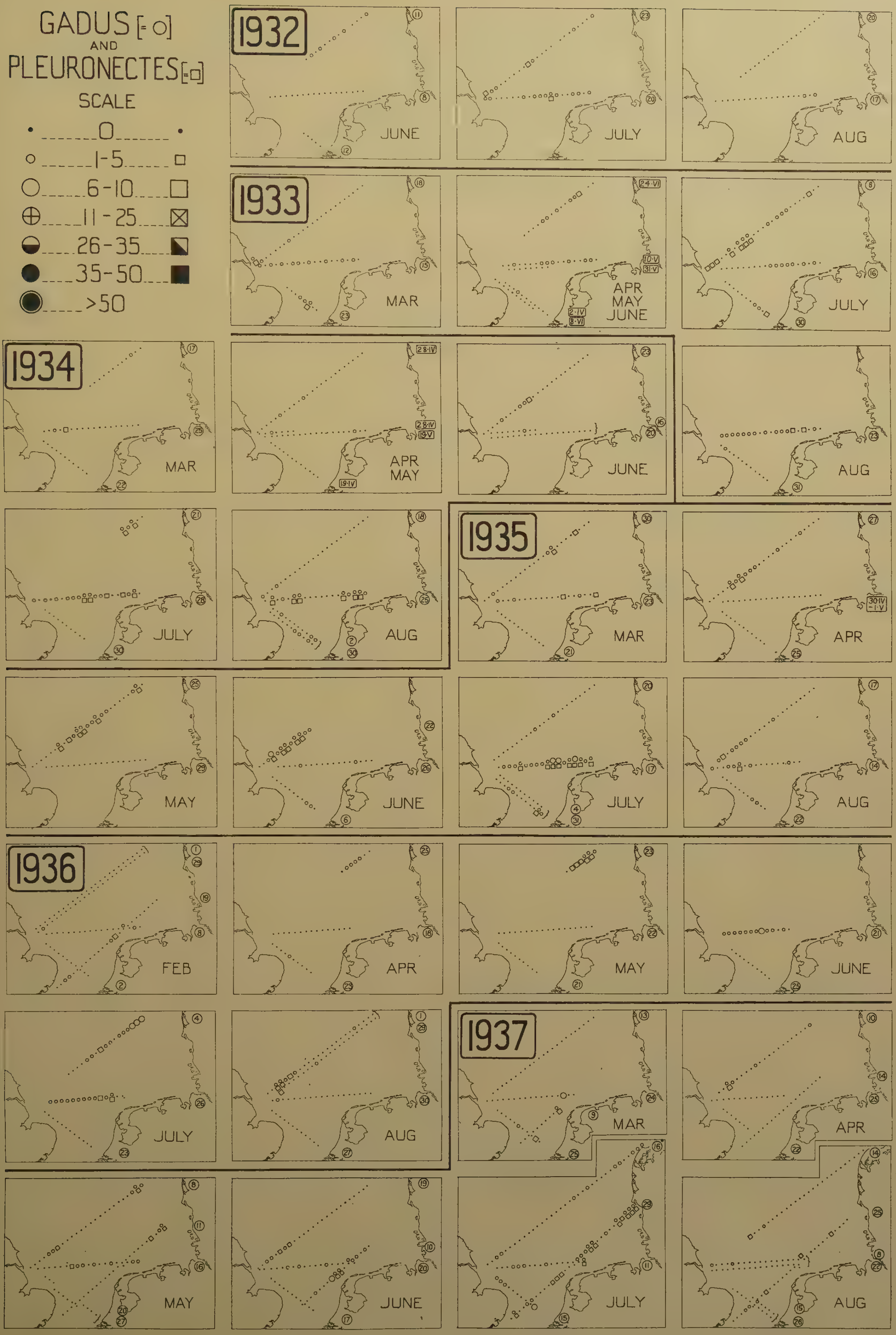
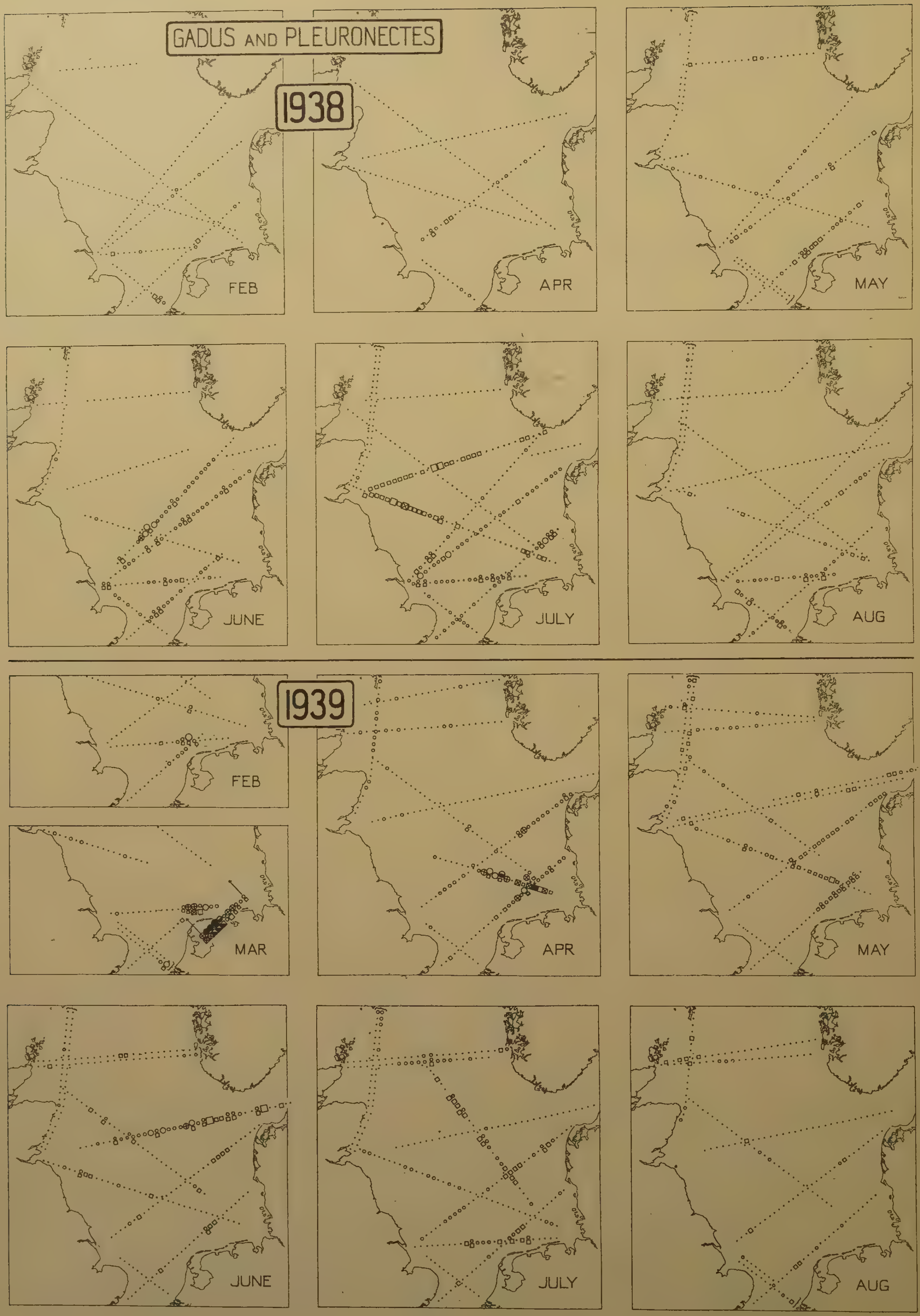

GADUS [= ○]
AND
PLEURONECTES [= □]
SCALE
• 0 •
○ 1-5 □
○ 6-10 □
⊕ 11-25 ⊠
◒ 26-35 ◩
● 35-50 ■
● >50
1932
JUNE
JULY
AUG
1933
MAR
APR MAY JUNE
24·VI
10·V
31·V
2·IV
8·VI
JULY
1934
MAR
APR MAY
28·IV
13·V
19·IV
JUNE
AUG
JULY
AUG
1935
MAR
APR
30·IV -1·V
MAY
JUNE
JULY
AUG
1936
FEB
APR
MAY
JUNE
JULY
AUG
1937
MAR
APR
MAY
JUNE
JULY
AUG

PLATE CXXIV


GADUS AND PLEURONECTES
1938
FEB
APR
MAY
JUNE
JULY
AUG
1939
FEB
MAR
APR
MAY
JUNE
JULY
AUG

[*Hull Bulletins of Marine Ecology, No. 16, Vol. II, pp. 283–293, July, 1951.*]

A STATISTICAL STUDY OF THE VARIABILITY OF CATCHES OBTAINED WITH TWO MODELS OF THE HARDY PLANKTON INDICATOR.

BY

H. BARNES, M.A., PH.D.
The Marine Station, Millport.

INTRODUCTION.

The use of a plankton indicator, designed originally to assist in the elucidation of the ecological relations of plankton and herring, was first suggested by Hardy (1925). The earliest model was kept below the surface by an attached weight, but a later type was fitted with a diving plane (Hardy and co-workers, 1936 and 1944), the paravane principle being used to keep the machine at a constant and known depth irrespective of considerable variations of towing speed. This paravane indicator has also been used by Gardiner (1933), and Gibbons and Fraser (1937) and Fridriksson (1944), and will be referred to as the " large " indicator. More recently a smaller model has been developed, similar in principle to the above indicator but of smaller overall dimensions. The opening of the " large " indicator is $1\frac{1}{2}$ in. in diameter and the diameter of the catching silk is 3 in. (ratio of areas 1 : 4), and the equivalent dimensions in the " small " model are $\frac{1}{2}$ in. and $1\frac{1}{4}$ in. respectively (ratio of areas 1 : 6).[1]

Herring investigations using these small indicators have recently been greatly expanded, and as a technique for similar ecological investigations it is becoming more widely adopted. Therefore it seemed advisable to make a statistical analysis of a series of replicate hauls, so that some assessment could be made of the sampling errors involved in the use of the Indicator. A series of tests (Series I–III) were initiated by the Department of Oceanography, University College, Hull. In addition to those workers supervising the tests other members of the Hull staff worked up the material, and thanks are due to them and to Mr. K. M. Rae for making the results available. Thanks are also due to the masters and crews of the vessels taking part for their helpful co-operation. As a result of the statistical work a further series of tests (Series IV) was made. For assistance in the boat work of Series IV the author wishes to express thanks to Captain Soutter and the crew of the M.V. " Calanus " of the Scottish Marine Biological Association.

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[1] A full account of this "small" indicator, which differs from the earlier model only in size and in minor points of construction, will be given later in this series by Mr. R. S. Glover.

The techniques involved in using indicators and in collecting and estimating the catches have already been described (Hardy *et alia, loc. cit.*), and this technique was used in Series I–III. In Series IV the catches were washed off the gauze disc after it had been carefully removed, and the whole sample counted ; in this series there are, therefore, no sub-sampling errors.

SERIES I.

In these tests, under the supervision of Mr. A. Saville of the Scottish Home Department's Marine Laboratory, Aberdeen, and made from F.R.V. " Explorer " in 1949, the " small " indicators were towed under good conditions during a routine cruise. The indicators used were taken from a large stock of these instruments. The three instruments were towed simultaneously, each tow being for 15 minutes at a nominal speed of 8 knots. During the tests one of the indicators became damaged and would not dive, so that it had to be replaced ; the results were therefore divided into two sections.

The plankton was not very abundant, and only two or three groups were numerous enough for use in an analysis. These were Calanus stages V and VI taken together, all other copepods taken together and Cladocera. The appropriate method of analysis of this type of data is that known as the analysis of variance (see Winsor and Clarke, 1940, for application to plankton sampling) and, as these authors point out, it is desirable to use logarithmic values of the catches in the analysis of variance, since the standard deviation tends to be proportional to the mean catch.

There were seven tows with the first three indicators, and only the second two groups of animals were taken in sufficient numbers for analysis. The mean population density was :

Total copepods	120 per tow per indicator.
Cladocera	443 ,, ,, ,,

(These values are given since other work has indicated that the true sampling variance is related to the population density, Barnes and Marshall, 1951.) The behaviour of these indicators as shown by the results of the analysis is given below, and in this first example the quantities of which the mean squares are estimates are also given, thus :

Source of variation.	Degrees of freedom.	Sum of squares.	Mean square.	Mean square is an estimate of—
Main Effects.				
Indicators (I)	2	0·3714	0·1857	$\sigma^2_0+t\sigma^2_{IG}+g\sigma^2_{IT}+tg\sigma^2_I$
Groups (G)	1	2·6195	2·6195	$\sigma^2_0+i\sigma^2_{GT}+t\sigma^2_{IG}+it\sigma^2_G$
Tows (T)	6	1·6794	0·2799	$\sigma^2_0+g\sigma^2_{IT}+i\sigma^2_{GT}+ig\sigma^2_T$
First Order Interactions.				
I × G	2	0·1315	0·0658	$\sigma^2_0+t\sigma^2_{IG}$
I × T	12	0·6727	0·0561	$\sigma^2_0+g\sigma^2_{IT}$
G × T	6	1·7279	0·2880	$\sigma^2_0+i\sigma^2_{GT}$
Second Order Interaction.				
I × G × T	12	0·4875	0·0406	σ^2_0
Total	41	—	—	

The indicators and tows will be considered random samples of these variables. Now the values for I × G and I × T are not significant (when tested against I × G × T), so that neither the proportion of the groups caught by the indicators over the tows nor the proportion (of all groups) caught by the indicators in the separate tows can be considered to differ significantly. However, G × T is significant, and probably indicates changes in the population sampled. The indicator mean square is not significant when tested against I × T, so that they did not behave differently over all the tows and groups. The high value of T appears to be largely due to a high G × T, so that T cannot be considered significant. The variance of a single observation, supposing an indicator were towed once and a group picked at random, will be the sum of the separate variance components. If a specified group is counted then the variation due to G, σ_G^2, will not contribute. In this first series after pooling the residual, the non-significant first order interactions and I, one has a new residual, with 16 degrees of freedom, of 0·0735. Since the value of T was not significant, the high value of T being dependent on that for G × T, further pooling gives an estimate of G × T of 0·2839. The estimate of the variance of a single observation is then found to give 0·1436. This corresponds to a log standard deviation of 0·3789 or a coefficient of variation of 139%.

In the second set of seven tows on this cruise (taken after replacement of the deficient indicator) all three groups were sufficiently abundant to give adequate numbers for analysis, the mean catches per indicator per tow being :

Calanus, stage V and VI	23
Total other copepods	535
Cladocera	211

The analysis of variance for this set gives :

Source of variation.	Degrees of freedom.	Sum of squares.	Mean square.
Main Effects.			
Indicators (I)	2	0·3483	0·1742
Groups (G)	2	20·79	10·40
Tows (T)	6	1·1989	0·1998
First Order Indications.			
I × G	4	0·0647	0·0162
I × T	12	1·6818	0·1402
G × T	12	3·4054	0·2838
Second Order Interaction.			
I × G × T	24	0·2958	0·0123
Total	62	—	—

Again I × G is not significant, but both I × T and G × T are significant when tested against I × G × T. After pooling the appropriate estimates, the variance of a single observation is obtained as 0·1456, corresponding to a coefficient of variation of 141%.

There is no information on the source of this significant I × T interaction. It might be suggested that it is dependent upon a connection between towing position and behaviour of the indicator. In these experiments, as in most of those described subsequently, the positions were assigned by randomization; but in any one set the number of tows were not large and a given indicator appeared in one position more than another, which, if behaviour and position were connected, would have influenced the results. However, inspection of the figures suggests that the effect is not positional; the mean catch for a given indicator in one position is little different from that in any other position, although the small number of tows in the same position makes definite conclusions impossible. Further in Series IV, where the indicators (which were different from those of Series I and II) were kept in the same position throughout, no significant I × T interaction is found. It is therefore difficult to ascribe the I × T interaction to other than experimental and uncontrolled error.

SERIES II.

These catches were made off Fraserburgh from the M.L. “Margaret” in 1948, and the tows were made under the supervision of Dr. G. T. D. Henderson. Each tow lasted 10 minutes, with the ship steaming at 8 knots. “Large” and “small” indicators (different from those of Series I) were towed simultaneously, but only the results from the two “small” indicators will be considered. There were five separate tows, and the following six groups were present in numbers sufficient for the analysis, the mean catch per tow per indicator being :

Calanus	20
Temora	50
Para- and Pseudocalanus together	91
Appendicularia	41
Gastropod larvae	122
Lamellibranch larvae	38

The analysis of variance gives—

Source of variation.	Degrees of freedom.	Sum of squares.	Mean square.
Main Effects.			
Indicators (I)	1	0·0926	0·0926
Groups (G)	5	4·5651	0·9130
Tows (T)	4	0·2606	0·0652
First Order Interactions.			
I × G	5	0·1319	0·0264
I × T	4	1·6647	0·4162
G × T	20	2·5463	0·1273
Second Order Interaction.			
I × G × T	20	0·7154	0·0358
Total	59	—	—

The results are very similar to the previous series, with a very high value for I × T and G × T again significant. An estimate of the variance of a single observation is 0·1443 corresponding to a coefficient of variation of 140%.

SERIES III.

These tows were taken from the S.D. "Corriedoune" during a fishing voyage off Fraserburgh in 1949, and were under the supervision of Mr. W. W. Brown. A different pair of indicators was used and each tow lasted 10 minutes. The depth of fishing was checked twice for each machine during the tests and the mean values were 3·15 and 3·05 fathoms for the two machines. Three groups only were present in sufficient numbers for analysis, these being :

Calanus, stages V and VI	57
Total other copepods	317
Cladocera	127

The analysis of variance gives—

Source of variation.	Degrees of freedom.	Sum of squares.	Mean square.
Main Effects.			
Indicators (I)	1	0·0048	0·0048
Groups (G)	2	5·0316	2·5158
Tows (T)	9	0·7166	0·0796
First Order Interactions.			
I × G	2	0·0755	0·0378
I × T	9	0·2580	0·0287
G × T	18	1·2044	0·0669
Second Order Interaction.			
I × G × T	18	0·2567	0·0143
Total	59	—	—

The mean squares are somewhat less then in the previous tests, the variability being less apparent. Apart from this the situation is much as in Series I. The variance of a single observation is 0·0458, corresponding to a coefficient of variation of 64%.

SERIES IV.

In the results just considered, the indicator tests were subsidiary to the main purpose of the cruise and it was therefore decided to repeat and extend these tests under more favourable conditions where the tests were the only object of the cruises. These subsequent tests were therefore done from M.V. "Calanus" in the Firth of Clyde, the weather being moderate to good throughout. All these tows were of 10 minutes' duration, with the ship steaming at a nominal speed of 8 knots; the positions of the indicators being towed simultaneously were allocated by random numbers.

(*a*) The three indicators used in the second part of Series I were first tested. The catch consisted almost entirely of several copepodite stages of a number of copepods. Since the results of the previous tests (I × G was never significant) had not suggested any differential effect with species only total counts were made. In these experiments the discs were transferred to bottles, the catch washed off, preserved and counted without sub-sampling. Nine separate tows were made, and the mean haul of total copepodites per indicator was 309. The analysis of variance gives the following :

Source of variation.	Degrees of freedom.	Sum of squares.	Mean square.
Main Effects.			
Indicators (I)	2	0·2299	0·1150
Tows (T)	8	0·6739	0·0842
Residual.			
I × T	16	0·06557	0·0410
Total	26	—	—

The values for indicators and tows are not significant, and an estimate of error of a single observation may be obtained by pooling these values and the residual. This gives a mean square of 0·0600, corresponding to a log standard deviation of a single observation of 0·2450 or a coefficient of variation of 76%.

(*b*) Two of the large indicators were then tested. Again only total copepod copepodites were counted and the conditions were as in (*a*). The mean catch per indicator per tow was 1137. The analysis of variance gives:

Source of variation.	Degrees of freedom.	Sum of squares.	Mean square.
Main Effects.			
Indicators (I)	1	0·0006	0·0006
Tows (T)	8	0·1158	0·0145
Residual.			
I × T	8	0·0255	0·0032
Total	17	—	—

Here the value of T is significant, and after evaluating it and adding to value for I × T one obtains for the variance of a single observation 0·0089, or a coefficient of variation of 24%.

A further series of tows was made with one of the large indicators used in the previous test and another large indicator (it would be difficult to tow three together.) The mean number per tow per indicator was 903. The analysis of variance gives:

Source of variation.	Degrees of freedom.	Sum of squares.	Mean square.
Main Effects.			
Indicators (I)	1	0·0114	0·0114
Tows (T)	5	0·1648	0·0330
Residual.			
I × T	5	0·0093	0·0019
Total	11	—	—

Here the values for I and T are both significant. The variance of a single observation is 0·0191 and the coefficient of variation is 38%.

A COMPARISON OF THE "SMALL" AND "LARGE" INDICATORS.

These tests were made off Fraserburgh by Dr. G. T. D. Henderson and Mr. A. Saville, on M.D. "Dundarg." Eight separate tows with "small" and "large" indicators towed simultaneously were taken, each tow lasting 15 minutes, at a speed of 8 knots. Two groups only were present in sufficient numbers for analysis, namely, Para- and Pseudocalanus taken together and Acartia. The mean ratio of the catches of the "large" to that of the "small" indicator was 0·700 (log. values), corresponding to a ratio of 5·01. The error to be attached to this ratio (obtained from the analysis of variance) indicated that for three standard deviation limits the ratio should lie between 8·21 and 3·06. The diameters of the openings of the machines are $1\frac{1}{2}$ in. and $\frac{1}{2}$ in., so that the ratio of the areas and the expected ratio of the catches, if both indicators are functioning efficiently, is 9 : 1. This lies outside the above limits, and it can be assumed therefore that the larger machine is catching significantly less in proportion to its opening than the smaller indicator.

The ratio of the area of opening to area of filtering gauze in the small machine is 1 : 6, but only 1 : 4 in the larger machine, and it appears possible therefore that the smaller ratio is not adequate for complete filtration. The filtering area of the silk may have too great a frictional resistance to pass the theoretical volume of water presented by the aperture when a certain amount of plankton is collected. This is in part confirmed by a second experiment carried out at a higher towing speed when the ratio of catches (mean of 3) was reduced to 3·6.

THE FILTRATION CAPACITY OF THE "SMALL" INDICATORS.

It was thought desirable to ascertain if the ratio of 1 : 6 was adequate for filtering the water, that is, if any increase in catch could be obtained by increasing the filtering surface. The normal gauze and disc was therefore replaced in one of the "small" indicators by a long net (area 42 cm.^{2}) fitted into the after end of the machine and trailing behind when towing. The area of opening to gauze was then 1 : 30, a value comparable to the ratio in the Hardy Plankton Recorders. Parallel tows were then made with a second "small" indicator fitted in the standard way with disc and gauze. The machines used were those tested in Series I and III, tows being taken in two separate pairs, the conditions and arrangements being as in Series IV. The mean catch of copepodite stages of all copepods per tow per indicator was 81. The analysis of the results from the first pair gives :

Source of variation.	Degrees of freedom.	Sum of squares.	Mean square.
Main Effects.			
Indicators (I)	1	0·1283	0·1283
Tows (T)	5	0·7243	0·1449
Residual.			
I × T	5	0·2274	0·0455
Total	11	—	—

The mean square for indicators is not significant, so that the same amount of catch is obtained whether large net or standard discs are used. In view of the large area of the nets, the above results strongly suggest that the standard gauze, under these conditions, filters the theoretical quantity of water. It should be noted that there was almost complete absence of any clogging of the silk by diatoms during this series.

A further similar test, in which the gauze and net were first in one indicator and then in the other, confirmed these results. There was no significant difference between the indicators under either conditions. The average number per indicator per tow was 237 in the first test and the analysis of variance gives :

Source of variation.	Degrees of freedom.	Sum of squares.	Mean square.
Main Effects.			
Indicators (I)	1	0·0702	0·0702
Tows (T)	3	0·0702	0·0234
Residual.			
I × T	3	0·0271	0·0090
Total	7	—	—

In the second test in which the other indicator had the net, and in which the mean catch per indicator per tow was 54, the analysis gives :

Source of variation.	Degrees of freedom.	Sum of squares.	Mean square.
Main Effects.			
Indicators (I)	1	0·0022	0·0022
Tows (T)	3	0·1310	0·0437
Residual.			
I × T	3	0·1056	0·0352
Total	7	—	—

Discussion.

A summary of the results is given in Table I. The coefficient of variation of the " small " indicator is of the same order as that (93%) given by Winsor and Clarke (1940) when pairs of their horizontal net hauls, taking half an hour, are considered. It should be noted that they were using nets 12·7 cm. in diameter towed in the standard way. This suggests that the indicators with their smaller openings give an adequate estimate of the population compared with that obtained using larger

TABLE I.

	Test.	Indicator.	Coefficient of variation.
I*a*	F.R.V. " Explorer "	" Small "	139
Ib	,,	,,	141
II	M.L. " Margaret "	,,	140
III	" Corriedoune "	,,	64
IVa	M.V. " Calanus "	,,	76
VIb	,,	" Large "	24
VIc	,,	,,	38

nets. In order to establish this point it would, however, be necessary to compare the two when towed simultaneously so that the distribution and nature of the plankton was in both cases identical. That different types of plankton animals may behave differently (due, for example, to different powers of movement) would also have to be considered.

The values of the coefficient of variation in the first two series are high and similar, whilst Series III and the small indicator comparisons of Series IV are smaller and also similar. Perhaps the large value of the earlier results is due to the tows being taken under " routine " conditions, whilst more attention was given to the tests in the later series. The earlier values may therefore be more representative of the variability to be expected when used by fishing vessels. It is also perhaps a reflection of a changing population, and this is substantiated by the high value of the G × T interaction, which reflects changes in the proportions of the groups counted with the tows. Certainly in Series IV this effect might have been reduced by towing in a restricted area and not, as in Series I, taking tows *en route* during a cruise.

The significant I × T interaction has already been discussed. Observations during the tests suggest that some of this variability is due to the light character of the indicators, slight damage (*e.g.*, bending of the parts) during use affecting their stability in towing. On this hypothesis the better behaviour of the larger and more robust machines could be explained.

As Winsor and Clarke have pointed out when dealing with these large percentage errors, it is better to make critical comparisons directly on the logarithms, and, if numerical upper and lower fiducial limits are required, to find these for the logarithms and then convert if necessary.

The order of variability may be indicated by obtaining 95% fiducial limits from the log standard deviation as calculated by Silliman (1946) for his pilchard egg data. (See, however, Sette and Ahlstrom, 1948.) For a single count from a single tow, and taking 75% as a representative coefficient of variation from the later series, then the limits are roughly 33 and 300%, so that one count could not be considered significantly different from another one unless it was less than one-third or more than three times its value. Only further work can show how far these limits are generally applicable, but the available evidence suggests that for similar organisms at similar population densities the results may be regarded as representative for this type of sampling technique. These results should therefore help to show those workers who wish to interpret results obtained by this method of sampling where significance can be inferred with some confidence.

Summary.

The variability of catches taken with two models of the Hardy Plankton Indicator has been examined statistically.

The 'coefficients of variation' and the relevant limits given by the two standard deviation values have been determined. The values are not greater than those reported for horizontal net hauls.

A comparison of the catching power of the two types and experiments in which the filtering-surface of the small indicator was increased have been reported. These results suggest that the small indicator filtered the " theoretical " quantity of water, but that the size of disc of the " large " indicator is not adequate for complete filtration.

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